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A TAXONOMIC REVISION OF *Jesús Muñoz*²
GRIMMIA SUBGENUS
ORTHOGRIMMIA (MUSCI,
GRIMMIACEAE)¹

ABSTRACT

Grimmia subg. *Orthogrimmia* comprises nine species distributed on mountain chains or high latitudes mainly in the Northern Hemisphere. This subgenus is defined by the following combination of characters: leaves V-shaped in transverse section, margins flat (seldom recurved in *G. reflexidens*), proximal marginal cells with the transverse walls thicker than the longitudinal walls, setae erect and straight (curved only in *G. arenaria*), and capsules symmetric and smooth. I recognize two sections: sect. *Donniana*, including *G. arenaria* Hampe, *G. donniana* Sm., and *G. triformis* Garestia & De Not.; and sect. *Montanae*, comprising *G. alpestris* (F. Weber & D. Mohr) Schleich., *G. caespiticia* (Brid.) Jur., *G. montana* Bruch & Schimp., *G. nivalis* Kindb., *G. reflexidens* Müll. Hal., and *G. ungeri* Jur. *Grimmia brachyphylla* Cardot, considered by other authors to be synonymous with *G. montana*, is shown to be conspecific with *Coscinodon humilis*, and is here lectotypified. *Grimmia sinensianodon* is considered to be synonymous with *Coscinodon cribrosus*, and not with *G. caespiticia*, as previously believed. All taxa are keyed and described, and typified where indicated. Illustrations and distribution maps are provided for each species.

Grimmia Hedw. is the largest genus in the Grimmiaceae (Musci). It is distributed throughout the world, mostly in mountainous areas. Several infrageneric taxa have been proposed within *Grimmia*, always based on the European species.

Grimmia subg. *Orthogrimmia* differs from the

other subgenera of *Grimmia* by the following combination of characters: leaves keeled, V-shaped in transverse section; margins flat (rarely recurved in *G. reflexidens*); proximal marginal cells with the transverse walls thicker than the longitudinal walls; setae erect and straight (curved only in *G. arenaria*);

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and capsules ovoid to fusiform, symmetric, and smooth. I have recognized two sections: sect. *Donniana*, with three species, and sect. *Montanae*, with six. The species of this subgenus are distributed along mountain chains mainly in the Northern Hemisphere. Only *G. reflexidens* is also known from the Southern Hemisphere.

The taxonomic history of *Grimmia* has been reviewed in an excellent manner by Deguchi (1978: 123–126). Table 1 summarizes several major taxonomic treatments of the genus.

Recently, revisions of *Grimmia* have been published for the Altai Mountains (Ignatov & Cao, 1994), China (Cao & Vitt, 1986), Europe (Grevén, 1995; Maier & Geissler, 1995), Japan (Deguchi, 1978), and South America (Deguchi, 1984, 1987). However, much more work must be done to resolve the taxonomic and nomenclatural difficulties of this genus.

Traditionally, the species dealt with in the present work have been treated (Hagen, 1909; Limpricht, 1890; Loeske, 1913) in *Grimmia* subg. *Guembelia* (Hampe) Schimp. (Schimper, 1856). However, the lectotype of *Guembelia*, designated by Pfeiffer (1874: 1511), is *Grimmia elliptica* Funck (nom. illeg. = *G. ovalis* (Hedw.) Lindb.), which belongs to a different subgenus, usually known by the later and arguably illegitimate name *Grimmia* subg. *Litoneuron* I. Hagen (Hagen, 1909). Therefore, *Grimmia* subg. *Guembelia* is the oldest name for the group usually known as subgenus *Litoneuron*, and the group usually known as subgenus *Guembelia* must be called *Grimmia* subg. *Orthogrimmia* Schimp., here lectotypified by *G. donniana* Sm.

The species in the *G. alpestris*–*G. donniana* complex of subgenus *Orthogrimmia* have been treated at various taxonomic ranks in the literature. Whereas *G. alpestris*, *G. caespiticia*, *G. donniana*, *G. montana*, and *G. reflexidens* (as *G. sessitana*) have usually been considered worthy of specific rank, *G. arenaria*, *G. nivalis*, *G. triformis*, and *G. ungeri* have rarely merited more than subspecific recognition. Nevertheless, all are discrete entities, without morphological intergradations. These taxa vary across their geographical ranges, but always in secondary features, mostly quantitative and presumably habitat-induced. These quantitative features have been much employed in the literature, yielding disparate taxonomies. On the other hand, major structural characters, such as presence or absence of stomata, have usually been neglected. From *Index Muscorum* (Wijk et al., 1962, 1969) onward, all the species treated in this study have been commonly lumped with *Grimmia donniana* following Habeeb (1950: 75). His knowledge of the group, however, was in-

adequate, as noted by Crum and Anderson (1981: 429).

MATERIALS AND METHODS

This revision is based on 1939 specimens from BCB, BCC, BM, BP, CANM, COLO, FH, G, GLM, H, JE, KRAM, KUN, LE, LISU, M, MA, MO, MUB, NY, OP, PAV, PC, S, TCD, TNS, TRH, VIT, W, WRSL, Z, as well as from the private herbaria of J.-P. Frahm (Bonn), E. Fuertes (Madrid), and R. B. Pierrot (Dolus). Some type specimens requested from DR, GLM, LZ, MPU, and ROST were not found in these herbaria.

Specimens were moistened in water with domestic detergent and then transferred to clean water. At the beginning of this study and, later, for types and specimens not immediately referable to any taxa, 10 to 15 mature but green leaves from the apical part of the stem (excluding the uppermost ones), transverse sections, the two or three innermost perichaetial leaves, and a capsule sectioned in eight parts were mounted in lactophenol gel (Zander, 1983) or Hoyer's (Anderson, 1954) medium. In this treatment, seta length includes the vagina. Lamina length excludes hair-point, lamina width has been measured at the broadest part of the leaf, and fractions (e.g., "margin recurved in the proximal 1/2") always refer to lamina length. Cell measurements include the wall. Proximal paracostal and marginal cells refer to the two or three rows of cells closest to the costa and margin, respectively.

I have distinguished species on the basis of morphological characters. They are "taxonomic species" according to Grant (1981: 78–80). The characters employed are important throughout the genus, and even the family.

For mapping distributions I have used ArcView GIS, which almost automatically loads geographical coordinates from database files with the ".dbf" format. Distribution maps are based solely on examined herbarium specimens. In "Selected specimens examined" I have cited only one specimen per geographical unit, and the total number of specimens parenthetically at the head of the section. A complete list of specimens studied is available upon request.

I have designated lectotypes for all names except those for which the author specifically selected in the protologue a single collection as holotype (Greuter et al., 1994, ICBN 9.1). The common practice of accepting as holotype a specimen kept in the personal herbarium of the original author can be a source of error. Good examples of problematic

Table 1. Various infrageneric divisions of *Grimmia*. An asterisk (*) indicates taxa that include species dealt with in this work.

Bruch & Schimper (1845)	Schimper (1856)	Lamprecht (1890)	Kindberg (1893) (ranks not indicated)	Hagen (1909)	Loeske (1930)
<i>Grimmia</i>	<i>Grimmia</i>	<i>Grimmia</i>	<i>Grimmia</i>	<i>Grimmia</i>	<i>Grimmia</i>
Tribu <i>Curtisetae</i>			<i>Sreptophyllum</i>	subg. <i>Gasterogrimmia</i>	subg. <i>Gasterogrimmia</i>
sect. <i>Crinatae</i>	subg. <i>Gasterogrimmia</i>	subg. <i>Gasterogrimmia</i>	<i>Eugrimmia</i>		
<i>Pulvinatae</i>			<i>Molliformes</i>	subg. <i>Rhabdogrimmia</i>	subg. <i>Rhabdogrimmia</i>
<i>Trichophyllae</i>	subg. <i>Grimmia</i>	subg. <i>Rhabdogrimmia</i>	<i>Velutinae</i> *		subg. <i>Pulvinatae</i>
<i>Elatiores</i>		subg. <i>Grimmia</i> *	<i>Pulvinatae</i> *		subg. <i>Torquatae</i>
<i>Ucinatae</i>			<i>Alpestriformes</i> *		
			<i>Andraeoroidae</i>		
		subg. <i>Guembelia</i> *	<i>Pseudocaracomitrium</i>		
			<i>Papillariae</i>		
			<i>Crispulae</i>		
Tribu <i>Rectisetae</i>			<i>Trichophylloideae</i> *	subg. <i>Litoneuron</i>	subg. <i>Litoneuron</i>
sect. <i>Leucophaea</i> *	subg. <i>Orthogrimmia</i> *		<i>Ovatiaeformes</i> *	subg. <i>Guembelia</i> *	subg. <i>Alpestris</i> *
sect. <i>Communitatae</i> *	subg. <i>Guembelia</i> *		<i>Unicoloriformes</i> *	sect. <i>Montanae</i> *	subg. <i>Alpinae</i>
				<i>Ovales</i> *	
				<i>Funales</i>	
			<i>Pseudo-Schistidium</i>		
			<i>Piliferiae</i> *		
			<i>Crinatae</i>		
<i>Aratae</i>		<i>Drypodon</i>		subg. <i>Streptocolea</i>	<i>Drypodon</i>
				subg. <i>Hydrogrimmia</i>	<i>Hydrogrimmia</i>
<i>Schistidium</i>	subg. <i>Schistidium</i>	<i>Schistidium</i>	<i>Schistidium</i>	subg. <i>Schistidium</i>	<i>Schistidium</i>
			<i>Platyphylloideae</i>		
			<i>Apocarpaeformes</i>		

typification are the many epithets associated with Kindberg or Müller (also cf. Ortiz, 1989).

TAXONOMIC CHARACTERS

This character overview refers to members of *Grimmia* subg. *Orthogrimmia*, except where otherwise indicated.

GAMETOPHYTE

Habit. The plants grow in dense compact cushions on rocks, mainly siliceous. These cushions are usually round and semi-spherical, although when growing in rock crevices they adopt the form of the crevice. The color of the plants varies among nuances of olive-green above, and usually blackish below.

Stem. Stems of *G. triformis* may reach 2 cm high, but most species rarely exceed 1.5 cm. The stem diameter varies between 100 and 210 μm . Stem internal structure in *Grimmia* was studied in depth by Kawai (1965: 113–117) and Deguchi (1978: 128–131). Kawai distinguished three parts in transverse section: an epidermal layer, a cortical layer, and a central strand. According to the degree of differentiation among the three layers, Kawai defined four stem types: "a" type, with no differentiation among the three layers, because of their nearly uniform cells; "b" type, where the epidermal and cortical layers are differentiated but the central strand is not; "c" type, where all three layers are differentiated and the central strand has less than 15 cells; and finally "d" type, as in the previous type but with a more developed central strand, i.e., of more than 15 cells.

Deguchi's system varies from that of Kawai. He joined Kawai's types "c" and "d" into his "Type II," whereas his Types "I" and "III" are identical to Kawai's types "a" and "b," respectively.

In this study the internal structure of the stem in *Grimmia* subg. *Orthogrimmia* was found to be characterized by a weak differentiation between the epidermal and cortical layers (which together form a more or less homogenous layer) on the one hand, and the central strand (which is well developed in nearly all species) on the other. This stem structure is intermediate between Kawai's types "a" and "c" or Deguchi's "I" and "II."

Branching. Branching systems in *Grimmia* have been studied in depth by Deguchi (1978: 128, figs. 1, 2). Branching pattern is usually sympodial, and this is the only type observed in *Grimmia* subg. *Orthogrimmia*. Innovations arise at the base of the perigonia and perichaetia. When these sexual structures are abundant, the stems appear like

stairs (Deguchi, 1978: figs. 1, 2). Occasionally, the plants appear monopodial because damaged sexual structures have fallen off. This is especially true for old plants. Rarely, the perigonia can be monopodially attached in cladoautoicous species.

All species of subgenus *Orthogrimmia* except *Grimmia caespiticia* show intricately branched stems resulting in a cohesive net and compact cushions. *Grimmia caespiticia* has less extensively branched stems, and its cushions are easily decomposed.

Some young branches have rhizoids at their base and are easily detached from the stems. This could reflect their role as diaspores in nature (Correns, 1899: 102; Deguchi, 1978: 128).

Rhizoids. Usually, rhizoids are limited to the base of stems. Plants subject to periodic inundation, however, have rhizoids throughout the stem length.

Axillary hairs. Axillary hairs in subgenus *Orthogrimmia* consist of 3–8 hyaline, uniseriate cells, of which the 1–2 most proximal ones are shorter. Length may vary between 50 and 175 μm .

Leaf orientation. When dry, all taxa have erect and appressed leaf bases, whereas the apex can be incurved and appressed (e.g., *G. caespiticia*, *G. montana*, and *G. ungeri*), variously flexuous (e.g., *G. arenaria*, *G. donniana*, and *G. triformis*) or appressed (e.g., *G. alpestris*, *G. nivalis*, and *G. reflexidens*). When moist, the leaves vary from erect to spreading, and *G. montana* exhibits sigmoid leaves in lateral view.

Leaf size and shape. Leaf lengths fall into two groups: shorter than 1.5 mm (e.g., *G. alpestris*, *G. caespiticia*, *G. montana*, *G. nivalis*, *G. reflexidens*, and *G. ungeri*); and longer than 1.5 mm (e.g., *G. arenaria*, *G. donniana*, and *G. triformis*). Mean leaf width is more uniform than length, always around 0.35 mm.

Grimmia alpestris, *G. caespiticia*, *G. nivalis*, *G. reflexidens*, and *G. ungeri* (Figs. 8a, b, 10a, 14b, 16a, 18a) have ovate leaves, with a length/width ratio of 2–3:1. *Grimmia arenaria*, *G. donniana*, *G. triformis*, and *G. montana* (Figs. 2a, 4a, 6a, 12a, b) have narrowly ovate leaves, with a length/width ratio of 3–6:1.

Leaf margin. The leaf margins are entire in all species studied, and plane at the base on both sides in most species. An exception to this rule are some populations of *G. reflexidens*, with recurved margins in the proximal half on one side and at the very base on the other side, or occasionally only briefly and narrowly recurved at the base on one side. Unfortunately, in this taxon it is an inconsistent character used profusely in the literature. The distal

leaf margins are plane or incurved. Exceptions are the mucous leaves of *G. caespiticia*, *G. montana*, and *G. nivalis*, which have a more or less cucullate apex.

Leaves in transverse section. Three types of leaves can be distinguished in *Grimmia* according to the shape of their transverse sections: concave, U-shaped (= canaliculate) and V-shaped (= keeled, carinate). Species in subgenus *Orthogrimmia* have strongly keeled leaves, although *G. montana* and more often *G. ungeri* can have only slightly keeled leaves in some populations.

Grimmia alpestris, *G. nivalis*, and especially *G. caespiticia* have leaves with a longitudinal plication on each side of the costa. The cells of these plicae are usually longer and narrower and have thicker walls, although they can be undifferentiated, mainly in the two former species.

Species of subgenus *Orthogrimmia* have a semiterete costa mostly projecting on the dorsal surface and clearly delimited from the lamina. Costal cross sections consist of three cell layers: ventral epidermis, internal band of stereids or substereids, and dorsal epidermis. Based on the morphology and differentiation of these three layers, Kawai (1965: 111, 1968: 128) recognized four types of costal structure in *Grimmia*. Species in subgenus *Orthogrimmia* belong to Kawai's "C" type, characterized by a more or less clear differentiation of the three layers, and a ventral epidermis two cells wide. Whereas costal structure and morphology are of great taxonomic value in some taxa of Grimmiaceae (e.g., *Racomitrium*, *Dryptodon*, other *Grimmia* subgenera), they have a limited utility in *Grimmia* subg. *Orthogrimmia*.

The leaf lamina is unistratose in the proximal part and 2(3–4)-stratose in the distal $\frac{1}{2}$ – $\frac{2}{3}$, mainly at the margins.

Laminar cells. The distal cells vary greatly in length, width, wall thickness, and sinuosity, and cannot be used to distinguish species. Their shape varies from isodiametric to rectangular or transversely rectangular in the same leaf, without any definite pattern. Length of major diameter ranges between 4 and 8 μm in *G. montana* and 8 and 13 μm in *G. alpestris*. Cell cross-sectional shape, on the other hand, is of great importance in defining taxa: *Grimmia alpestris*, *G. caespiticia*, *G. nivalis*, and some populations of *G. reflexidens* have rounded cells bulging on both surfaces, whereas *G. arenaria*, *G. donniana*, *G. triformis*, *G. montana*, and *G. ungeri* have isodiametric or rectangular cells plane on the lamina surface (seldom *G. montana* has cells slightly bulging on the dorsal surface). *Grimmia nivalis* and many populations of *G. caes-*

piticia have papillose distal laminar cells. The papillae are usually better developed on the dorsal than on the ventral surface.

The proximal laminar cells in *Grimmia arenaria*, *G. donniana*, and *G. triformis* are alike: hyaline, and long and narrow (length/width ratio 3–10:1). Their walls are thin and even, straight and nearly indistinct, although the paracostal cells can have somewhat thickened and sinuous walls (Figs. 2e, 4c, 6c). *Grimmia alpestris*, *G. caespiticia*, *G. montana*, *G. nivalis*, *G. reflexidens*, and *G. ungeri* have proximal cells that range from isodiametric to rectangular (to 6:1 in paracostal cells), with the transverse walls always thicker than the longitudinal ones, which usually are thicker than in the other species of the subgenus (Figs. 8d, 10c, 12d, 14e, 16e, 18d).

Hair-points. As in almost any other species in the genus, the length of the hyaline hair-points varies significantly in subgenus *Orthogrimmia*, and can often be correlated with ecological conditions. Populations from exposed habitats usually have longer hair-points. *Grimmia arenaria* has the longest hair-points in the subgenus despite habitat, and they are always strongly flexuous. *Grimmia caespiticia*, a species of exposed sunny and dry habitats, has the shortest hair-points, at times reduced to as few as one hyaline cell. Male plants of dioicous species always have shorter hair-points than their female counterparts, and when cushions of different sexes grow intermingled, they can appear quite distinct.

The hair-points are usually erect, and their degree of flexuosity depends on their length. Short hair-points are straight, whereas longer ones are often flexuous. *Grimmia arenaria* always has strongly flexuous and homomalous hair-points.

In *Grimmia alpestris*, *G. caespiticia*, *G. montana*, *G. nivalis*, *G. reflexidens*, and *G. ungeri* the hair-points are always terete, whereas in *G. arenaria* and *G. triformis* they are always flat. The structure of the hair-points in *G. donniana* depends on their length: longer hair-points are flat, whereas shorter ones are more or less terete.

Perichaetial leaves. The inner perichaetial leaves of most species of subgenus *Orthogrimmia* are well differentiated from the apical vegetative ones, i.e., they are 2–3 times larger and convolute. Moreover, the cells in the proximal, sheathing half are enlarged and hyaline-yellowish, with very thin walls, at least along the margins. Exceptions are *G. arenaria*, with undifferentiated perichaetial leaves, and *G. caespiticia*, with convolute but only slightly larger perichaetial leaves.

The hyaline hair-points are always longer in perichaetial than in vegetative leaves.

Reproductive organs. Taxa in subgenus *Orthogrimmia* are dioicous, gonioautoicous (androecium bud-like and axillary on the same stem as the terminal gynoecium) or cladautoicous (androecium on a separate stem). In the last-mentioned case, ramifications and the growth of branches at times produce a notable separation of perichaetium and perigonium-bearing branches. In this case, the plants could seem dioicous.

Androecia can be axillary or terminal. The latter are easy to observe, since they are inflated and bulbiform, giving the stem a clavate appearance. Axillary buds are smaller and very difficult to find, especially in autoicous species. The antheridia are surrounded in both types by strongly differentiated, cochleariform perigonal leaves with acute apices.

Perichaetia are always terminal, but soon appear axillary due to elongation of the subfloral branch (Deguchi, 1978: figs. 1, 2).

SPOROPHYTE

Autoicous species, i.e., *G. arenaria*, *G. donniana*, *G. reflexidens*, *G. triformis*, and *G. ungeri*, had sporophytes in 70–100% of the studied collections. Dioicous species show important differences in the percentage of fertile collections: *Grimmia nivalis* had sporophytes in all examined samples except one, *Grimmia alpestris* showed a high percentage, near 90%, whereas *G. caespiticia* and *G. montana* exhibited lower percentages, ca. 70%.

Setae. The setae are straight except in *G. arenaria*, which has curved setae. Other species can occasionally have slightly curved setae, particularly *G. reflexidens*. The setae are longer than capsules in all species except *G. triformis*. They range in length from 1 mm in *G. triformis* to 4 mm in *G. alpestris* and *G. montana*. In all species the seta is twisted counterclockwise when dry.

Capsules. Capsules provide important taxonomic characters in subgenus *Orthogrimmia*. Recently dehisced or, better, non-dehisced capsules must be used. Older capsules have greater deposits of wax over their exothelial cells, and most are infected by fungi, making it difficult to recognize important features, like the presence of stomata or the thickness of the exothelial cell walls.

All species of subgenus *Orthogrimmia* have smooth capsules. They are exserted except in *Grimmia arenaria*, which has emergent capsules, and *G. triformis*, which has immersed capsules.

Capsules are mostly ovoid, with a wide base abruptly connected to the seta. The only exception

is *G. alpestris*, with ellipsoid-fusiform capsules attenuated at the base and not abruptly connected with the setae (Fig. 8c). The base is usually symmetrical, but in some populations of *G. alpestris*, *G. montana*, and *G. reflexidens* the base is slightly asymmetrical and the capsule is weakly inclined.

Capsules of *Grimmia arenaria*, *G. donniana*, *G. reflexidens*, *G. triformis*, and *G. ungeri* are usually stramineous, although in the last two species the color can turn to brownish in older capsules. The capsule color of *G. alpestris*, *G. caespiticia*, *G. montana*, and *G. nivalis* is castaneous.

At the capsule mouth there are several rows of small, transversely rectangular, usually reddish or brownish, more intensely colored cells with thick walls. This character is uniform in subgenus *Orthogrimmia*. The cells of the rest of the urn are isodiametric, rectangular, or transversely rectangular; usually all types are present, with one of them dominating. The exothelial cell walls are thin (less than 3 μm) in *G. arenaria*, *G. caespiticia*, *G. donniana*, *G. montana*, *G. reflexidens*, and *G. ungeri*, and thick (more than 3 μm) in *G. alpestris*, *G. nivalis*, and *G. triformis*.

Stomata can be found in the neck region of the urn in all species of subgenus *Orthogrimmia* except *G. alpestris*, *G. montana*, and *G. ungeri*. The best procedure for observing the stomata is to cut a capsule in half and then cut the proximal half again (for a total of four parts) and search for stomata (in uncut old capsules it can be hard to see the stomata because of secondary deposits of wax and other substances). The guard cells are reniform, and under the compound microscope appear dotted or colored, with a cellular content different from that of the adjoining exothelial cells. The cells surrounding the guard cells are usually undifferentiated from the other exothelial cells, thus the stomata can be classified as anomocytic. Sometimes, however, the row of subsidiary cells surrounding the guard cells is slightly differentiated and smaller than the other exothelial cells, and such stomata could be considered stephanocytic (Baranova, 1987).

The absence of stomata is a good character to separate *Grimmia alpestris* from the closely related *G. nivalis* and *G. reflexidens*.

Two annular types can be recognized in subgenus *Orthogrimmia* (Deguchi, 1978: 143–144). Annulus cells in the *Schistidium*-type are undifferentiated from the exothelial rim cells and non-revolvible. All species in section *Montana* have this type of annulus (simple and persistent). On the other hand, the *elongata*-type is characterized by having two or three rows of isodiametric, inflated

and hyaline, revolvable cells. All species in section *Donnianae* have this type of annulus (compound and revolvable).

The peristome of *Grimmia* subg. *Orthogrimmia* consists of 16 more or less entire, irregularly divided or cribrate teeth. Their width, measured at the outer surface of the peristome base, varies from 35–50 μm in *G. caespiticia* and *G. ungeri* (Figs. 10d, 18f) to 70–100 μm in *G. triformis* (Fig. 6f). The teeth are densely papillose on the inner surface, whereas on the outer surface they are papillose distally and smooth or slightly papillose proximally. Tooth color (castaneous-brown or orange) is constant in each species.

The operculum is conic with a short mammilla in all species except *G. montana*, in which it is rostrate.

Calyptrae. Calyptra morphology is much employed in the taxonomy of Grimmiaceae. All species in *Grimmia* subg. *Orthogrimmia* have smooth calyptrae, which may be mitrate (sect. *Donnianae*) or cucullate (sect. *Montanae*). Only one collection of *Grimmia donniana* out of the 555 fertile specimens of section *Donnianae* studied had some cucullate calyptrae, and I considered this an abnormality.

Spores. The spores of all species of subgenus *Orthogrimmia* are spherical and homogenous in size (isosporic, Mogensen, 1983: 334–336). Under the compound microscope they appear smooth, but are minutely granulose (Cao & Vitt, 1986: fig. 16c, f). Hirohama (1978: 37, figs. 57, 58) described the spores as smooth, but his figures show a minutely granulose surface similar to Cao and Vitt's figure 16c.

Once again, it is possible to separate the group consisting of *G. arenaria*, *G. donniana*, and *G. triformis* (i.e., sect. *Donnianae*), with smaller spores (6.5–11.0 μm), from that comprising *G. alpestris*, *G. caespiticia*, *G. montana*, *G. nivalis*, *G. reflexidens*, and *G. ungeri* (i.e., sect. *Montanae*), with larger spores (9–14 μm).

CHROMOSOME NUMBERS

It has been pointed out that the basic chromosome number in Grimmiaceae is $x = 7$ (Smith, 1978; Vitt, 1984). From this number have been derived the remaining ones in the family: 10, 12, 12+m, 13, 13+m, 14, 14+1–4acc., 22, 26, and 26+m (Fritsch, 1991; Vaarama, 1949).

The most common haploid complement in *Grimmia* is $n = 13$, with $n = 10$, 12+m, 13+m, 14, and 14+1–4acc also common. These numbers were probably derived through doubling of the basic x

= 7 complement of the Grimmiaceae (primary diploids). Other species have a haploid complement of $n = 26$ or $n = 26+m$ (Fritsch, 1991), probably resulting from secondary doubling of the $n = 13$ chromosome complement (secondary diploids).

It is generally acknowledged that the duplication of the chromosome number implies a directional transformation from a dioicous to an autoicous sexual condition [but see Wyatt & Anderson (1984) for a thorough discussion on this topic]. Ramsay (1983: fig. 147, see also discussion on pp. 202–206) diagrammed the various ways of maintaining the dioicous condition by aneuploid reduction. Some of the primary diploids in *Grimmia* may have reverted to the dioicous sexual condition (e.g., *G. alpestris*), whereas others have become autoicous (e.g., *G. arenaria* and *G. donniana* (Fig. 1)).

Chromosome counts for the species studied here are scarce (Table 2). Known numbers are $n = 13$ or 13+m for *G. alpestris*, $n = 12+m$ and $n = 13$ for *G. donniana*, and $n = 13$ for *G. arenaria* and *G. montana*. I was only able to verify the identity of the voucher for the count of *G. donniana* (Khan, 1964: 348, fig. 5).

TAXONOMIC TREATMENT

Grimmia Hedw., Sp. Musc. Frond. 75. 1801.

TYPE: *Grimmia plagiopodia* Hedw. (lectotype, designated by Mårtensson (1956: 106–107).

Autoicous or dioicous. Plants in dense cushions or compact to loose tufts, glaucous, green, greenish yellow, or dark green. *Stems* erect or ascending, with or without central strand. *Leaves* erect, appressed or flexuous, occasionally with homomallous tips when dry, erect to spreading when moist, linear, ovate, lanceolate, ligulate or oblong, obtuse to acuminate, concave, canaliculate or keeled, plane or plicate; *margins* entire, plane, recurved or incurved; *costa* single, percurrent, terete, semi-terete, semi-elliptic, or almost indistinct in cross section; *lamina* 1- to 4-stratose in the distal half, smooth or pseudopapillose; *distal cells* isodiametric to rectangular or transversely rectangular, with straight or sinuous walls, plane or bulging, smooth or papillose; *proximal cells* isodiametric to rectangular or transversely rectangular, the walls straight or sinuous, uniformly thickened or with the transverse walls thicker than the longitudinal walls; with or without *hyaline hair-points*. *Perichaetial leaves* convolute and larger, or similar in shape but slightly larger than vegetative leaves; *hyaline hair-points* entire to dentate, or lacking. *Androecia* axillary or terminal. *Setae* straight, curved, or coiled, longer or shorter than capsules. *Capsules* immersed, emer-

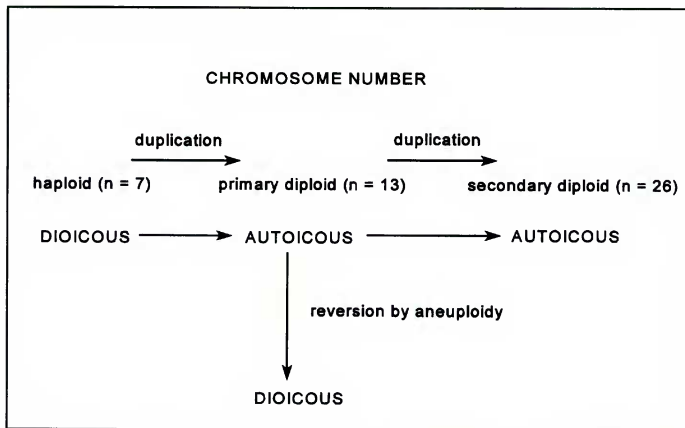


Figure 1. Correlation between chromosome number and sexual condition in *Grimmia*.

gent or exerted, subglobose, ovoid, ellipsoid, or fusiform, symmetric or asymmetric and ventricose at the base, smooth or furrowed, stramineous or castaneous; with stomata at the urn base or lacking stomata; *exothecial cells* isodiametric to rectangular, thin- or thick-walled; *annulus* simple and persistent or compound and revolute, of 1–3 rows of isodiametric to rectangular cells; *peristome teeth* 16, triangular, entire, perforate in the distal half or cribrate throughout their length and irregularly cleft in the distal $\frac{2}{3}$ – $\frac{3}{4}$, orange or brown; *opercula* conic to long-rostrate; *calyptrae* mitrate or cucullate, smooth, covering the operculum; *columella* persistent; *spores* usually 8–16 μm , occasionally up to 20 μm , smooth to granulose.

The supraspecific taxonomy of *Grimmia* has yet to be fully resolved. Whereas some recognized supraspecific taxa (cf. Table 1) are natural and well established (e.g., subgenera *Grimmia* and *Orthogrimmia*), others are at present tentative. The following key is intended to separate subgenus *Orthogrimmia* from all other members of *Grimmia*, not to present a taxonomy of the genus. No formal status or circumscription is given to either “*Rhabdogrimmia*” or “*Alpinae*” until further work on these groups is carried out.

KEY TO MAJOR SUPRASPECIFIC TAXA OF *GRIMMIA*

- 1a. Capsules strongly asymmetric at base, ventricose
..... *Grimmia* subg. *Grimmia*

Table 2. Chromosome numbers reported for *Grimmia* subg. *Orthogrimmia*.

Species	$n =$	Origin	Author
<i>Grimmia alpestris</i>	13	California	Steere et al. (1954)
	13+m	Georgia (Republic)	Lazarenko et al. (1971)
	13	Colorado	Khanna (1971)
<i>Grimmia arenaria</i>	13	Great Britain	Smith & Newton (1968)
<i>Grimmia donniana</i>	12+m	New York	Khanna (1964)
	13	Great Britain	Smith & Newton (1966)
	13	Great Britain	Ramsay (1969)
	13	Kazakhstan	Vysotskaya & Lesnyak (1984)
	13	Poland	Kuta et al. (1984)
<i>Grimmia montana</i>	13	Canada	Anderson & Crum (1958)

- 1b. Capsules symmetric or very slightly asymmetric, not ventricose at base.
 - 2a. Setae variously curved; capsules mostly ribbed, or if smooth, leaf margins recurved to some degree or leaves variously crisped "Rhabdogrimmia"
 - 2b. Setae straight or, if curved, capsules smooth, leaf margins plane and leaves straight to flexuous, not crisped.
 - 3a. Leaves concave; costa semi-elliptic, indistinct *Grimmia* subg. *Guembelia*
 - 3b. Leaves canaliculate to keeled; costa semi-terete, clearly delimited from lamina.
 - 4a. Leaf margins plane or incurved *Grimmia* subg. *Orthogrimmia*
 - 4b. Leaf margins recurved.
 - 5a. Annulus compound and revolvable "Alpinae"
 - 5b. Annulus simple and persistent *Grimmia* subg. *Orthogrimmia* (*G. reflexidens*)

Grimmia subg. **Orthogrimmia** Schimp., Coroll. Bryol. Eur. 48 1856. TYPE: *Grimmia donniana* Sm. (lectotype, here designated).

Autoicous or *dioicous*. Plants in dense, compact tufts, glaucous, green, greenish yellow, or dark green. *Stems* erect, to 2 cm tall \times 110–210 μ m diam., with central strand well developed, sometimes with rhizoids present nearly throughout; *axillary hairs* 3–8-celled, hyaline, 50–175 μ m long. *Leaves* erect, appressed to flexuous (occasionally with homomallous tips) when dry, erect-spreading to spreading (occasionally sigmoid in lateral view), flaccid or rigid when moist, 0.8–2.2 \times 0.25–0.65 mm, narrowly ovate to ovate, acute to acuminate, keeled, although sometimes only weakly, plane or plicate; *margins* plane, seldom recurved; *costa* semi-terete in cross section, usually prominent on the dorsal surface, slightly to clearly delimited, with 2 cells in the ventral epidermis, an internal band of steroids or substereids, and a dorsal epidermis, the three layers \pm differentiated; *lamina* 2–3(4)-stratose in the distal half, mainly along the

margins, smooth or pseudopapillose; *distal cells* 4–20 \times 7–14 μ m, isodiametric to short or transversely rectangular, with straight or sinuous walls, plane or bulging, smooth; *proximal paracostal cells* 10–55 \times 7–20 μ m, green, isodiametric to rectangular (1–6:1), the walls straight or sinuous, uniformly thickened or the transverse walls thicker than longitudinal walls; *proximal marginal cells* 9–50 \times 6–20 μ m, isodiametric to rectangular (1–5:1), with transverse walls thicker than longitudinal cell walls; or *proximal and paracostal cells* 35–100 \times 5.5–25 μ m, alike, hyaline, long and narrow (3–10:1), with even, very thin, straight, scarcely discernible walls; *hyaline hair-points* flat or terete at the base, somewhat to strongly flexuous, at times homomallous and twisted, to 2 mm long, denticulate to dentate. *Perichaetial leaves* 1.5–3.1(–4) \times 0.4–0.9 mm, convolute and larger (2–3 \times) or similar in shape but slightly larger than vegetative leaves; *hyaline hair-points* plane or terete, flexuous, to 2.8 mm, entire, denticulate or dentate. *Androecia* axillary or terminal. *Setae* straight or curved, to 1.0–4.5 mm long. *Capsules* immersed, emergent or exserted, ovoid, ellipsoid or fusiform, symmetric (seldom slightly asymmetric at base), smooth, stramineous or castaneous; with stomata at the urn base, or lacking stomata; *exothelial cells* 16–70 \times 10–55 μ m, isodiametric to rectangular (1–4.5:1), thin- or thick-walled; *annulus* simple and persistent or compound and revolvable of 2–3 rows of mostly isodiametric cells 6–10 μ m high; *peristome teeth* 35–100 μ m wide at the base, entire, perforate in the distal half or cribrate throughout their length and irregularly cleft in the distal $\frac{3}{4}$ – $\frac{3}{4}$, orange or brown, concolorous or contrasting in color with the urn, outer surface papillose distally and smooth or slightly papillose proximally, inner surface papillose throughout; *opercula* conic to rostrate; *calyptrae* mitrate or cucullate. *Spores* 6.5–14 μ m, minutely granulose.

Distribution. All continents.

KEY TO SECTIONS OF GRIMMIA SUBG. ORTHOGRIMMIA

- 1a. Proximal marginal cells of leaf \pm hyaline and inflated, length/width ratio 3–10:1, walls thin, scarcely discernible, the transverse walls similar to the longitudinal walls; calyptrae mitrate; annulus compound and revolvable I. *Grimmia* subg. *Orthogrimmia* sect. *Donniana*
- 2a. Setae straight, to 1 mm; capsules immersed; exothelial cells thick-walled 3. *G. triformis*
- 2b. Setae straight or curved, longer than 1 mm; capsules emergent or exserted; exothelial cells thin-walled.
 - 3a. Setae curved; hyaline hair-points to 2 mm, those of the perichaetial leaves strongly flexuous and twisted 1. *G. arenaria*
 - 3b. Setae straight; hyaline hair-points to 1 mm, those of the perichaetial leaves weakly flexuous and not twisted 2. *G. donniana*
- 1b. Proximal marginal cells of leaf neither hyaline nor inflated, length/width ratio 1–4.5(6):1, walls thick, always distinct, the transverse walls thicker than the longitudinal walls; calyptrae cucullate; annulus simple and persistent II. *Grimmia* subg. *Orthogrimmia* sect. *Montanae*
- 4a. Laminar cells not bulging (Figs. 12e, 16d, 18c).

- 5a. Stomata present at the urn base 8. *G. reflexidens*
 5b. Stomata lacking.
 6a. Opercula long-rostrate; setae 2–4 mm long; peristome teeth 50–90 μm wide at mouth, irregularly splitting above and \pm cribrate; proximal paracostal leaf cells mostly long-rectangular, to 4.5:1; dioicous 6. *G. montana*
 6b. Opercula obtuse to mammillate; setae to 2 mm; peristome teeth 40–50 μm wide at mouth, entire or slightly cribrate at apex; proximal paracostal leaf cells isodiametric to rectangular, to 2:1; autoicous 9. *G. ungeri*
 4b. Laminar cell bulging (Figs. 8e, 16c).
 7a. Laminar cells papillose.
 8a. Leaves strongly plicate on both sides of costa 5. *G. caespiticia*
 8b. Leaves plane or weakly plicate 7. *G. nivalis*
 7b. Laminar cells not papillose.
 9a. Leaves strongly plicate on both sides of costa 5. *G. caespiticia*
 9b. Leaves plane or weakly plicate.
 10a. Stomata lacking at the urn base; capsules usually fusiform, castaneous, concolorous with peristome teeth; exothelial cells isodiametric, thick-walled 4. *G. alpestris*
 10b. Stomata present at the urn base; capsules ovoid, stramineous, different in color from the orange peristome teeth; exothelial cells irregularly rectangular, thin-walled 8. *G. reflexidens*

I. *Grimmia* (subg. *Orthogrimmia*) sect. *Donniana* (Loeske) J. Muñoz, comb. et stat. nov. *Grimmia* [unranked] *Donniana* Loeske, Biblioth. Bot. 101: 110. 1930. TYPE: *Grimmia donniana* Sm.

Autoicous. Plants in compact tufts, green, greenish yellow, or dark green. *Stems* to 2 cm tall, with central strand well developed, sometimes rhizoids present nearly throughout; *axillary hairs* 3–7-celled, 70–160 μm long. *Leaves* erect and appressed or flexuous (occasionally with homomallous tips) when dry, patent to spreading, and flaccid or rigid when moist, 1.3–2.2 \times 0.25–0.65 mm, narrowly ovate, acute to acuminate, keeled, plane; *margins* plane; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half, smooth or pseudopapillose; *distal cells* 7–11 \times 7–14 μm , isodiametric to rectangular or transversely rectangular, plane, smooth; *proximal paracostal and marginal cells* 35–100 \times 5.5–25 μm , alike, hyaline, narrowly rectangular (3–10:1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* flat or terete at the base, somewhat to strongly flexuous, at times homomallous and twisted, to 2 mm long, denticulate to dentate. *Perichaetial leaves* 1.8–3.1 \times 0.4–0.8 mm, convolute and larger (2–3 \times) or similar in shape but slightly larger than vegetative leaves; *hyaline hair-points* plane, flexuous, to 2.8 mm, entire, denticulate or dentate. *Androecia* axillary or terminal. *Setae* straight or curved, to 3.5 mm long. *Capsules* immersed, emergent or exerted, ovoid or ellipsoid, symmetric, smooth, stramineous, with stomata at the urn base; *exothelial cells* 30–70 \times 10–46 μm ,

isodiametric to rectangular (1–4.5:1), thin- or thick-walled; *annulus* compound and revoluble of 2–3 rows of isodiametric cells 6–12 μm high; *peristome teeth* 50–100 μm wide at the base, entire, perforate in the distal half or cribrate throughout, irregularly cleft in the distal $\frac{3}{4}$ – $\frac{3}{4}$, orange, contrasting in color with the urn; *opercula* conic or with a short mammilla; *calyptrae* mitrate. *Spores* 6.5–11 μm .

Distribution. Northern America, Europe, and temperate Asia.

Grimmia subg. *Orthogrimmia* sect. *Donniana* is characterized by thin-walled proximal marginal cells, mitrate calyptrae, and a compound and revoluble annulus.

- 1. *Grimmia arenaria*** Hampe, Linnaea 10: 405. 1836. *Grimmia curvula* Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 113, tab. 238. 1845, nom. illeg. incl. sp. prior. *Grimmia incurva* Schleich. ex Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 113. 1845, nom. inval. pro syn. *Grimmia donniana* var. *curvula* Spruce, Musci pyrenaici n° 281, 1847. *Grimmia donniana* subsp. *arenaria* (Hampe) Dixon, Stud. Handb. Brit. Mosses Ed. 2: 155. 1904. *Grimmia donniana* var. *arenaria* (Hampe) Loeske, Laubm. Eur. Part I: 93, figs. 1c, 17a, 26b, 28. 1913. TYPE: [Germany, Magdeburg:] Regenstein Hercyn[iae], June, *Hampe s.n.* (lectotype, here designated, BM; isolectotype, FH).

Illustrations. Figure 2; Bruch et al. (1845: tab. 238, sub *G. curvula*).

Autoicous. Plants in hoary tufts, dark-green to blackish. *Stems* to 1.5 cm tall, with central strand

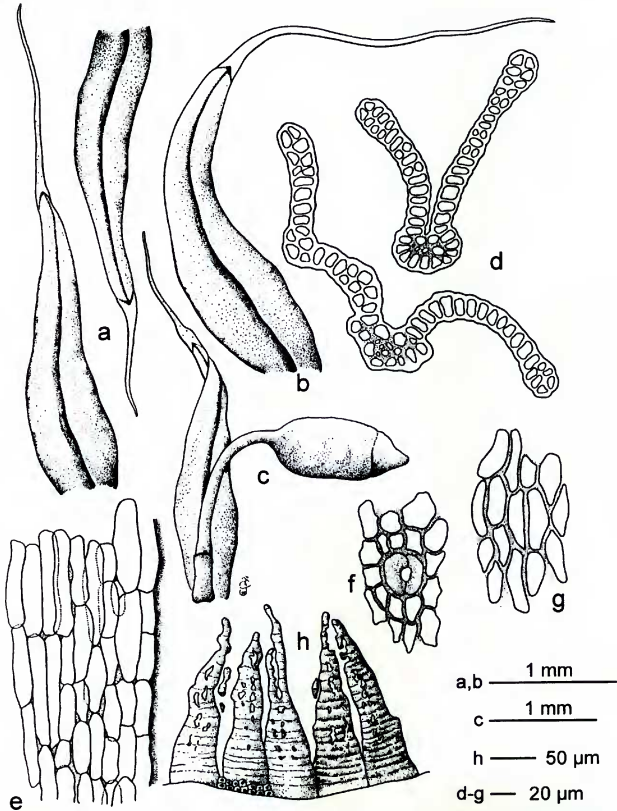


Figure 2. *Grimmia arenaria*. —a. Leaves. —b. Perichaetial leaf. —c. Sporophyte and perichaetial leaf. —d. Transverse sections of leaf. —e. Proximal leaf cells. —f. Proximal exothelial cells and stoma. —g. Medial exothelial cells. —h. Annulus and peristome teeth. [a, d–h, *Garovaglio s.n.* (G); b, *Spruce*, Musci Pirenaici n° 281, (TCD).]

well developed; *axillary hairs* 5–7-celled, 140–160 μm long. *Leaves* erect (occasionally with the tips homomallous) when dry, patent to spreading, flaccid when moist, $1.3\text{--}2.2 \times 0.25\text{--}0.65$ mm, narrowly ovate, acute to acuminate, keeled, not plicate; *margins* plane; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half, occasionally pseudopapillose; *distal cells* 7–10 μm , trans-

versely rectangular to isodiametric or rectangular, plane, smooth; *proximal paracostal and marginal cells* $35\text{--}95 \times 8\text{--}25$ μm , alike, hyaline, narrowly rectangular (3–10:1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* flat, strongly flexuous, usually homomallous and twisted, to 2 mm long, rarely shorter than 1 mm, denticulate to dentate. *Perichaetial leaves* 1.8–

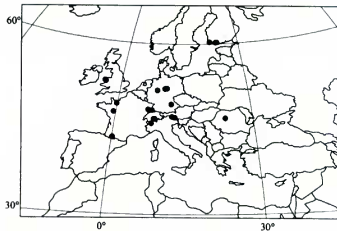


Figure 3. Distribution of *Grimmia arenaria*.

2.6 × 0.4–0.7 mm, similar to vegetative leaves but slightly larger; *hyaline hair-point* similar to those of vegetative leaves but longer, to 2.8 mm. *Androecia* terminal. *Setae* curved, ca. 2 mm long. *Capsules* exerted or, more commonly, emergent among the perichaetial leaves, ovoid, symmetric, stramineous, with stomata at the urn base; *exothecial cells* 30–55 × 10–20 μm, rectangular (1.5–4.5:1), thin-walled; *annulus* compound and revolute of 2–3 rows of isodiametric cells 10 μm high; *peristome teeth* 50–90 μm wide at the base, perforate in the distal part, eroded and irregularly divided in 2–3 branches, orange, contrasting in color with the urn; *opercula* conic or mammillate; *calyptra* mitrate. *Spores* 6.5–10.5 μm.

Diagnostic characters. (1) Proximal laminar cells hyaline, thin-walled. (2) Hyaline hair-points very long, to 2 mm, twisted and usually homomalous. (3) Capsules emergent and facing down among the perichaetial leaves. (4) *Setae* short and curved. (5) Annulus compound and revolute. (6) Peristome teeth 50–90 μm wide at the base, perforate in the distal part, eroded and irregularly divided in 2–3 branches.

Distribution (Fig. 3). Central and western Europe, Finland, and Great Britain; open areas from 10 to 1800 m elevation, on dry sandstone and slate. Mature sporophytes were present in 100% of the studied specimens.

This species is distinguished at first sight by the curved setae and small ovoid capsules emerging among the long and twisted hair-points.

With more than half (ca. 68%) of the samples studied from the vicinity of Regenstein (Germany), the type locality, low variability may be expected. Indeed, this taxon varies only in the length of the hyaline hair-points, which only rarely is less than 2 mm. Even the shorter points are strongly curled and flexuous, a feature not seen in other species of the subgenus.

Grimmia arenaria has been treated mostly as an infraspecific taxon of *G. donniana*, both as a subspecies (e.g., Dixon, 1904: 155) and a variety (e.g., Podpěra, 1954: 280). Only recently have Greven (1994, 1995: 44–47) and Touw and Rubers (1989: 212–213) agreed with Limpricht's (1890: 735–736) view that this taxon should be treated at the specific level.

Selected specimens examined (155). AUSTRIA. **Carinthia:** im Kressbrunngraben bei Raibl, *Breidler s.n.* (BP-36050). **Tirol:** Innervillgraten, *Gander s.n.* (BP-36053). FINLAND. **Turku ja Pori:** Lojo, Karkalinniemi, 5 Aug. 1880, *Lindberg s.n.* (G). FRANCE. **Isère:** mt. de Isans, Aug. 1800, *Ravaud s.n.* (TRH). **Maine-et-Loire:** Angers, *Schimper s.n.* (S). **Pyrénées Centrales:** in fauce dict. la Gorge de Labassère, *Spruce s.n.* (NY). **Vosges:** Le Hohneck, *Boulay s.n.* (FH). GERMANY. **Baden-Württemberg:** Südl. Schwarzwald, nahe südwarde du Gipfel des Schauinsland, Aug. 1925, *Schmidt s.n.* (JE). **Magdeburg:** Blankenburg, Regenstein, 23 Mar. 1902, *Janzen s.n.* (JE). ITALY. Biellese ne' monti dell'Oropa e di S. Giovanni d'Andorno, Aug. 1861, *Cesati s.n.* (G). ROMANIA. Siebenbürgen, Alpe Paring, *Péterfi s.n.* (BP-36055). SPAIN. **Lérida:** Vallferrera, *Casas s.n.* (IBA-3952). SWITZERLAND. **Tessin:** Fusio, July 1908, *Trautmann s.n.* (S). UNITED KINGDOM. **Wales:** Merioneth, Talsarnan, Harlech, Sep. 1911, *Rhodes s.n.* (S).

2. *Grimmia donniana* Sm., Engl. Bot. 18: pl. 1259. 1804. *Grimmia sudetica* Schwägr., Sp. Musc. Frond. Suppl. 1(1): 87, tab. 24. 1811, nom. illeg. incl. sp. prior. *Grimmia donni* Gray, Nat. Arr. Brit. Pl. 1: 728. 1821, nom. illeg. *Dryptodon donnianus* (Sm.) Hartm., Handb. Skand. Fl. Ed. 3: 270. 1838. *Grimmia obtusa* var. *donniana* (Sm.) Hartm., Handb. Skand. Fl. Ed. 5: 377. 1849 (1850?). *Grimmia donii* Sm. ex Lindb., Musci Scand. 30. 1879, nom. illeg. *Grimmia donniana* var. *eudonniana* Loeske, Laubm. Eur. Part I: 91. 1913, nom. inval. *Gumbelia donniana* (Sm.) Loeske, Laubm. Eur. I: 90. 1913, nom. inval. *Grimmia donniana* subsp. *eudonniana* Giacom., Atti Ist. Bot. Lab. Crittog. Univ. Pavia, ser. 5, 4: 221. 1947, nom. inval. TYPE: [United Kingdom. Caernarvon:] North Wales, Beddgelart, July 1802, *Turner s.n.* (lectotype, here designated, BM).

Grimmia obtusa Schwägr., Sp. Musc. Frond. Suppl. 1(1): 88, tab. 25. 1811, nom. illeg., non Brid., 1801. *Grimmia donniana* var. *obtusa* (Schwägr.) Steud., Nomencl. Bot. 2: 189. 1824. *Dryptodon erostris* Hartm., Handb. Skand. Fl. Ed. 4: 374. 1843, nom. illeg. incl. sp. prior. TYPE: [Austria.] Glockner, *Kaulfuss s.n.* (holotype, G; isotype, G).

Grimmia sudetica Spreng. ex Schkuhr, Deutschl. Krypt. Gew. Heft 2: 48, Tab. 22. 1811. *G. donniana* f. *sudetica* (Spreng. ex Schkuhr) Loeske, Biblioth. Bot. 101: 113. 1930, nom. illeg., non Chal. 1882. TYPE:

[Poland. Sudety. *Ludwig* s.n.] "Kryptogamische Gewächse der Riesengebirgen. Laubmoose" [hand-written label, not the original of Ludwig's *exsiccata*] (lectotype, here designated, M).

Grimmia donniana var. *bohemica* Schkuhr ex Brid., Bryol. Univ. 1: 176. 1826. *Grimmia bohemica* Schkuhr ex Steud., Nomencl. Bot. 2: 188. 1824, nom. inval. pro syn. *Grimmia donniana* var. *bohemica* Schkuhr ex Steud., Nomencl. Bot. 2: 189. 1824, nom. inval. pro syn. TYPE: [Poland.] Schneekoppe Sudetum, 1814. *Ludwig* s.n. (lectotype, here designated, B).

Illustrations. Figure 4; Bruch & Schimper (1845: tab. 249, sub *G. obtusa*); Cao and Vitt (1986: figs. 15, 16a-c); Chalušičský (1882: tab. 7 fig. 11); Deguchi (1978: fig. 27); Ignatov and Cao (1994: fig. 10, but not figs. 8, 9); Jóhannsson (1993: fig. 32); Limpricht (1890: fig. 198); Noguchi (1988: fig. 140B); Nyholm (1956: fig. 69F).

Autoicous. Plants in tufts, greenish yellow above, dark green to blackish below. *Stems* to 1.5 cm tall, with central strand well developed; *axillary hairs* 4-5-celled, 90-125 μm long. *Leaves* erect and appressed (occasionally with the tips somewhat flexuous) when dry, patent and rigid when moist, 1.3-2.2 \times 0.25-0.60 mm, narrowly ovate, acute to acuminate, keeled, plane; *margins* plane; *costa* semiterete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose at margins and in streaks in the distal half, occasionally pseudopapillose; *distal cells* 7-11 \times 7-9 μm , isodiametric to rectangular (1-1.5:1), plane, smooth; *proximal paracostal and marginal cells* 38-80 \times 5.5-15.0 μm , alike, hyaline, narrowly rectangular (4-9:1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* terete or flat when longer, slightly flexuous, usually to 1 mm long (seldom to 2 mm and then strongly flexuous), smooth to weakly denticulate. *Perichaetial leaves* 2.0-2.5 \times ca. 0.8 mm, convolute and larger than vegetative leaves (2.0-2.5 \times); *hyaline hair-points* slightly flexuous when short, strongly so when longer, to 2.2 mm, smooth or denticulate. *Androecia* axillary or terminal. *Setae* erect and straight, to 3.5 mm long. *Capsules* exerted, ovoid, symmetric, smooth, stramineous, with stomata at the urn base; *exothecial cells* 35-55 \times 24-46 μm , isodiametric to rectangular (1-2:1), thin-walled; *annulus* compound and revolvable of 2-3 rows of isodiametric cells 10-12 μm high; *peristome teeth* 50-70 μm wide at the base, entire or weakly broken at the tips, orange, contrasting in color with the rest of the sporophyte; *opercula* conic or mammillate; *calyptrae* mitrate. *Spores* 7-11 μm .

Diagnostic characters. (1) Proximal laminar cells hyaline, thin-walled. (2) Hyaline hair-points to 1 mm, slightly flexuous, seldom longer (to 2 mm)

and then more flexuous. (3) Capsules exerted. (4) Setae straight, to 3.5 mm. (5) Annulus compound and revolvable. (6) Peristome teeth 50-70 μm wide at the base, entire or only slightly cleft at the tip.

Distribution (Fig. 5). Common in Europe, it is scattered through Siberia, Nepal, Japan, North America, and Greenland; open areas and forests from 80 to 3800 m elevation on all types of non-calcareous rocks. Mature sporophytes were present in 96.5% of the specimens studied.

Grimmia donniana is rather stenotypic and easy to recognize because of its hyaline proximal cells, straight setae, and exerted capsules. The most variable features are the length and twisting of the hair-points, but they are rarely as long and flexuous as in *G. arenaria*. However, I have studied two puzzling specimens in which the variation observed is difficult to interpret. *Chernyaljeva* 37 (Kamchatka, Kosheleva volcano, LE) exhibits some cucullate calyptrae, but this is the only deviant feature observed and is here considered an abnormality. Another anomalous specimen is *Sharp 4761 p.p.* (Mexico, Popocatepetl, TENN). It has the shortest setae seen in *G. donniana* (i.e., 1 mm) and the capsules are mostly immersed, approaching *G. triformis*. Nevertheless, it matches typical *G. donniana* in all other respects, especially in the thin-walled exothecial cells and the entire and narrow peristome teeth.

See comments under *Grimmia arenaria* and *G. triformis* for differences between these species and *G. donniana*.

Most collections from eastern North America identified as *G. donniana* are specimens of *G. incurva* Schwägr. with nearly straight seta and autoicous inflorescence. The latter species can be distinguished from *G. donniana* by its longer, narrower, and more acuminate leaves, which are crisped and contorted when dry.

Grimmia sudetica Schwägr. was considered the legitimate name for *G. alpestris* by Geissler and Maier (1995: 503). However, in the original publication, Schwägrichen (1811: 87) cited *G. donniana* as a synonym of his new species, which thereby became illegitimate (Muñoz, 1998).

Grimmia donniana has a non-continuous, circumboreal distribution. It is quite common in mountainous areas in central and northern Europe, but becomes rare toward the south and the east. In North America, it is known from scattered localities in the United States and Mexico. In Asia *Grimmia donniana* is rare, growing on Honshu (as cited hereunder) and Hokkaido (Deguchi, 1978: fig. 28), Japan, and from the Altai Mountains and Tibet in

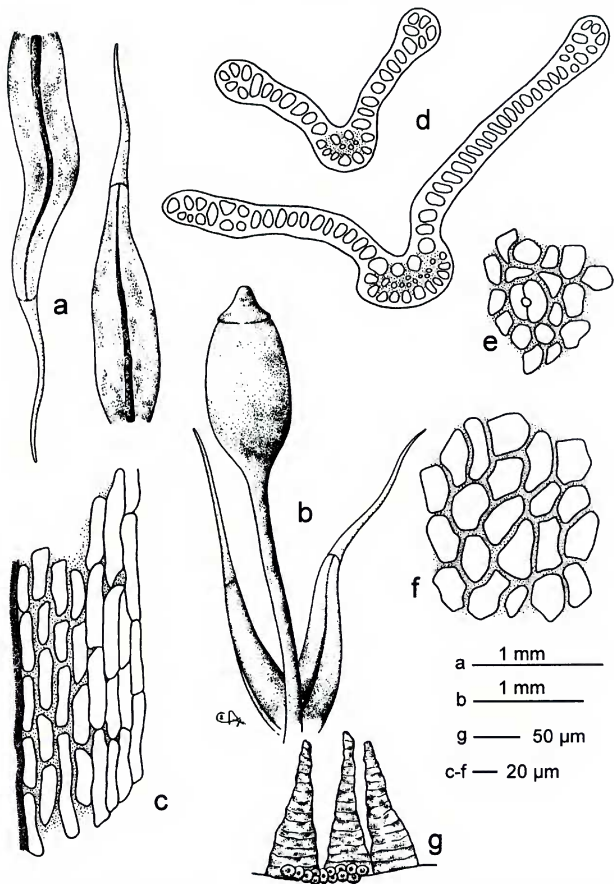


Figure 4. *Grimmia donniana*. —a. Leaves. —b. Sporophyte and perichaetial leaves. —c. Proximal leaf cells. —d. Transverse sections of leaf. —e. Proximal exothelial cells and stoma. —f. Medial exothelial cells. —g. Annulus and peristome teeth. [a–g, Turner s.n. (BM).]

continental Asia. Two of the three Tibetan reports (Cao & Vitt, 1986: 161) actually pertain to *G. elongata* Kaulf. (*Lang Kaiyong* 598, ALTA) and *G. longirostris* Hook. (*Lang Kaiyong* 5302, ALTA).

Grimmia donniana has also been reported from

Africa (Ochyra & Sharp, 1988: 344) and Antarctica (Bartram, 1957: 141; Kuc, 1969; Savicz-Lyubitskaya & Smirnova, 1969). However, the collections from these areas studied by me represent other taxa (e.g., *G. kidderi*, *G. lawiana*, or *G. reflexidens*).

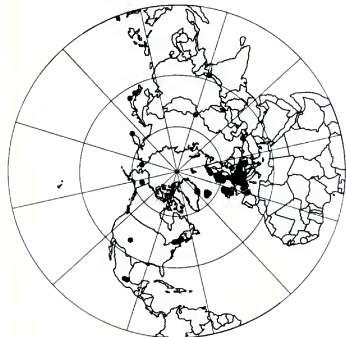


Figure 5. Distribution of *Grimmia donniana*.

Selected specimens examined (380). **AUSTRIA.** **Carinthia:** im Kremsthal, *Breidler s.n.* (BP-36075). **Salzberg:** Speiereck im Zimgau, 8 Aug. 1887, *Schliephacke s.n.* (GOET). **Steiermark:** im Schöttalgraben bei Oberwölz, *Breidler* (BP-36077). **Tirol:** Innervillgraten, 1 Sep. 1892, *Gander s.n.* (TRH). **CZECH REPUBLIC.** Bohemia, Montes Krkonoše, vallis Obří důl, Apr. 1949, *Pilous s.n.* (H); Riesengebirge, Felstrümmer der Schneekoppe, July 1887, *Limpricht s.n.* (RO); Tatra Magna, montis Nagymorgár, supra lacu Zelene pleso-Zöldöl, *Vajda s.n.* (BP-74869). **FRANCE.** **Vosges:** prope Lacum viridem, *Mougeot & Nestler s.n.* (FH). **Haute-Loire:** Le Mégal, *Wallace & Cuyvet s.n.* (BP-112577). **Puy-de-Dôme:** sous le sommet du Puy-de-Dôme, *Pierrot s.n.* (BP-112575). **Pyrénées Centrales:** au sommet du port d'Oo, 5 Sep. 1856, *Zetterstedt s.n.* (TRH). **Savoie:** Pralognan, cirque de l'Arceclin, *Parriat s.n.* (BP-112578). **GEORGIA.** **South Ossetia Autonomous Oblast:** Dzhavskij rajon, Ermani, 9 Sep. 1946, *Abramov s.n.* (LE). **GERMANY.** **Bavaria:** Bayerischer Wald, Arberkuppe, *Progel s.n.* (BP-36101). **Bayern:** auf dem Ochsenkopf, *Funck s.n.* (RO); bei Annaberg, *Weicker s.n.* (BP-36102). **Karl-Marx Stadt:** Bärenstein, *Kopsch s.n.* (BP-112572). **Magdeburg:** Regenstein bei Blankenburg, *Itzigsohn s.n.* 1843 (S). **Niedersachsen:** Oberharz, Luisenklippen auf dem Quitschenberg zwischen Torfhan und Oderbrücke, 11 July 1988, *Heimhold s.n.* (GOET). **Rhön:** Gipfel der Milseburg, *Anonymous s.n.* (BP-36108). **Saxonia:** prope Altenberg, *Rabenhorst s.n.* (BP-80338). **Thüringia:** *Schmidt s.n.* (GLM-2850). **HUNGARY.** Montes Szeben, prope Paltanis, *Vajda s.n.* (BP-73974). **ICELAND.** North Iceland, Bakrangei area, above farn Nipá, NE of Akureyri, 1 July 1964, *Steere s.n.* (NY); South Iceland, Skaftafell, *Aproot 4974* (NY); hill near Grötta bei Rejkjavik, *Andrews 1/2* (NY). **IRELAND.** Down, Mourne Mts., Slieve Donard, Ballagh Park, 15 Oct. 1884, *Lett s.n.* (TCD). **ITALY.** Mte. S. Gottardo, July 1853, *Franzoni s.n.* (RO); Rima, precipizii del Mte. Tagliaferro, 19 Aug. 1863, *Carestia s.n.* (RO). **JAPAN.** Toyama Prefecture, Mt. Tateyama, 11 Aug. 1955, *Iwatsuki s.n.* (G); prov. Iwashiro, mt. Iida, *Ishiba 1331* (H-BR). **NORWAY.** **Bergen:** Arstad, mellem Haulelandsvadnet og Kronstad, 9 Sep. 1871, *Wulfsberg s.n.* (TRH). **Kristians:** Lom, Bäv-

erdalen, Røshejm, 19 Aug. 1887, *Hagen s.n.* (FH). **Sondre Trondhjem:** Stören, Rognes, 16 July 1884, *Hagen s.n.* (TRH). **POLAND.** Between Wolowiec and Klin, *Chalubiński s.n.* (BP-36084); Beskidy Zachodnie Mts., Babia Góra Mt., ad declivitatem meridionalem sub cacuminem Głwniak, *Wojterski s.n.* (BP-112978); Sudetes Mts., Karkonosze Range, Jelenia Góra-Zaborze, *Prager s.n.* (BP-6071). **ROMANIA.** **Beszterce-Naszód:** Mt. Rodnai havasok, cacuminis montis Ünökő, *Péterfi s.n.* (BP-112955). **Brasov:** montes Fogarasi havasok, vallis Arpasul, *Vajda s.n.* (BP-70413). **Maramureş:** sept. jugi Lunca ciasa sub monte Toroiaga prope pagum Borsabánya, *Boros s.n.* (BP-112954). **Szeben:** Cibin, ad "Wasserleitungs-Weg" supra Hohe Rinne *Boros s.n.* (BP-112947). **RUSSIA.** **Gorno Al'tayskaya Autonomous Oblast:** Altai Mountains, Trekhlavaya Peak, *Zolotukhin s.n.* (IBA-7025). **Kamchatka:** slopes of Kosheleva volcano, *Chernyadjeva 37* (LE). **Magadan:** Chukotka peninsula, Lake Ioni, 5 July 1977, *Afonina s.n.* (LE). **SLOVAKIA.** **Gömör:** merid. montis Ókérhegy pr. Rozsnyó, *Boros s.n.* (BP-112915). **Špis:** in jugo "Lorenz-Joch" supra lacum "Wahlenberg See," *Dege s.n.* (BP-112900); Liptovské hole, *Kalivčiv. Pilous s.n.* (BP-112584). **SWEDEN.** **Nordvestra:** Härjedalens, Helagsfjället, Aug. 1913, *Smith s.n.* (TRH). **Sule Lappmark:** Rvihhjohk Njammsts, 15 July 1891, *Ryan s.n.* (IBA-4128). **SWITZERLAND.** **Unterwalden:** Engelberg, bei der Klostersennerei Seerenrütli, July 1859, *Cramer s.n.* (RO). **Tessin:** Fusio, July 1908, *Trautmann s.n.* (TRH). **Valais:** Vallon d'Arpettas, 30 Aug. 1889, *Bernet s.n.* (FH). **TIBET.** Yatong County, *Zang 669* (ALTA). **UKRAINE.** Ukrainian Carpathians, Chornogora range, Turkul Mt., *Partyka s.n.* (IBA-6993). **UNITED KINGDOM.** **England:** Cumberland, Grange, Apr. 1870, *Borrowdale s.n.* (FH). **Wales:** Carnarvonshire, Capel Curig, Feb. 1880, *Bleekell s.n.* (FH).

MEXICO. **México:** Popocatepetl, *Sharp 4761* p.p. (TENN). **Veracruz:** monte Orizaba, *Galeotti s.n.* (PC). **GREENLAND.** Runde Fjeld (the summit), 12 May 1892, *Hartz s.n.* (NY). **U.S.A.** **Alaska:** Circle Quadrangle; vicinity of Eagle Summit, mile 105-108 Steese Highway, *Steere 72-895* (NY). **Colorado:** Clear Creek Co., S side, Summit Lake, Mount Evans, *Weber 7769* (FH). **Maine:** Piscataquis Co., Abol Slide, W slope of mt. Katahdin, *Hermann 19276* (G). **New Hampshire:** Mt. Washington, 12 Aug. 1939, *Harring, Wickes & Grout s.n.* (FH). **New York:** Essex County trail from Adirondack Loj to Algonquin Peak of the MacIntyre Mountains, *Redfearn 13325* (MO).

3. *Grimmia triformis* Carestia & De Not., *Comment. Soc. Crittog. Ital.* 2: 102. 1866. *Grimmia donniana* var. *triformis* (Carestia & De Not.) Loeske, *Laubm. Eur. Part I*: 96, figs. 26d, 30. 1913. TYPE: [Italy, Vercelli.] In Tagliaferro, a qualche metro sotto la veta sul versante di Rima, 19 Aug. 1963, *Carestia s.n.* (lectotype, here designated, BM; isolectotypes, BM [2 replicates], BP-37541, JE).

Grimmia ganderi Limpr., *Jahresber. Schles. Ges. Vaterl. Cult.* 61: 215. 1884. *Grimmia donniana* var. *breviseti* Breidl. ex Loeske, *Laubm. Eur. Part I*: 95. 1913. TYPE: [Austria, Tirol, Innervillgraten, "Kalchstein" 4400 ft., 15 Mar. 1884, *Gander s.n.* (lectotype, here designated, BP-37547; isolectotypes, JE [2 replicates], H).

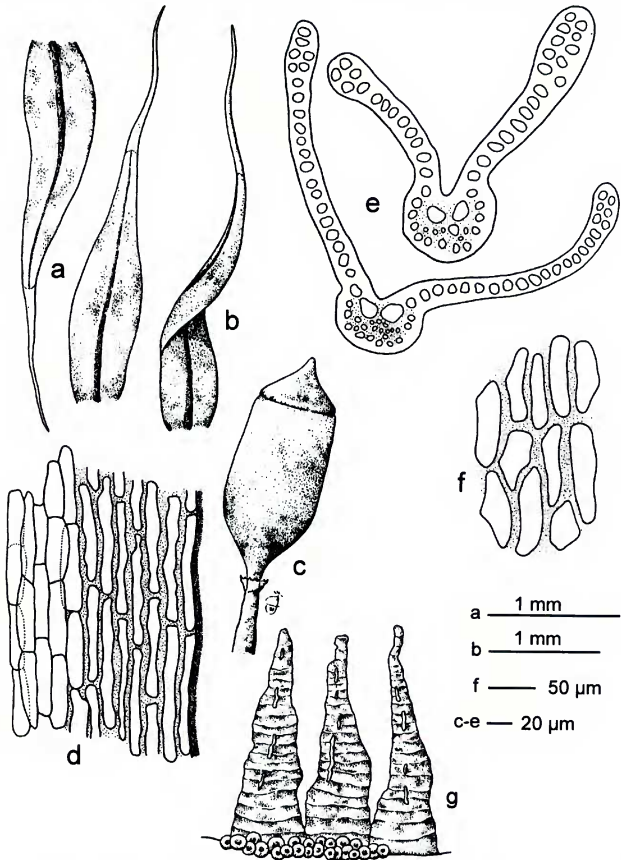


Figure 6. *Grimmia triformis*. —a. Leaves. —b. Perichaetal leaf. —c. Sporophyte. —d. Proximal leaf cells. —e. Transverse sections of leaf. —f. Medial exothecial cells. —g. Annulus and peristome teeth. [a, c, d, f, *Gander s.n.* (BP-37547); b, e, *Gander s.n.* (BP-37549).]

Illustrations. Figure 6; Ignatov and Cao (1994: fig. 5, sub *Coscinodon cribrus*); Limpricht (1890: figs. 196, 197).

Autoicous. Plants in tufts, green. Stems to 2 cm tall, with central strand weakly developed; rhizoids abundant to middle of stems; axillary hairs 3-

celled, ca. 70 μm long. Leaves erect and flexuous when dry, patent and flaccid when moist, 1.5–2.2 \times 0.3–0.5 mm, narrowly ovate, acute, keeled, plane; margins plane; costa semi-terete, prominent on the dorsal surface, clearly delimited; lamina 2-stratose at margins and in streaks in the distal half,

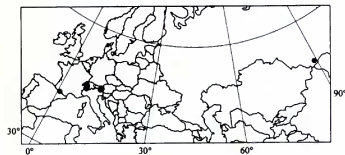


Figure 7. Distribution of *Grimmia triformis*.

occasionally pseudopapillose; *distal cells* 7–9 × 7–14 μm, isodiametric to rectangular (1–1.5:1), plane, smooth; *proximal paracostal and marginal cells* 40–100 × 7–18 μm, alike, hyaline, narrowly rectangular (3–10:1), with even, very thin, straight, scarcely discernible walls, or the paracostal cells with thickened and sinuous walls; *hyaline hair-points* flat, flexuous, to 1.3 mm long, denticulate. *Perichaetial leaves* 2.5–3.1 × 0.8 mm, convolute and larger than vegetative leaves, yellowish at the base; *hyaline hair-points* flat, strongly flexuous, to 2 mm, denticulate. *Androecia* terminal. *Setae* erect and straight, to 1 mm long. *Capsules* immersed, ovoid, symmetric, smooth, stramineous, with stomata at the urn base; *exothecial cells* 46–75 × 10–21 μm, irregularly rectangular (2–4:1), thick-walled; *annulus* compound and revoluble of 2 rows of isodiametric cells 6–10 μm high; *peristome teeth* 70–100 μm wide at the base, cribrate throughout and irregularly cleft in the distal 3/4, orange, contrasting in color with the urn; *opercula* conic or mammillate; *calyptrae* mitrate. *Spores* 8–11 μm.

Diagnostic characters. (1) Proximal laminar cells hyaline, thin-walled. (2) Capsules immersed. (3) Setae erect and straight and very short (to 1 mm). (4) Annulus compound and revoluble. (5) Peristome teeth 70–100 μm wide at the base, cribrate throughout and irregularly cleft in the apical 3/4.

Distribution (Fig. 7). Very rare, known only from the European Alps and Pyrénées, and from an outlying locality in the Altai Mountains of Siberia; in open areas above the tree-line between 1385 and 4500 m elevation on non-calcareous rocks. Mature sporophytes were present in 100% of the specimens studied.

This seldom-collected taxon hardly varies, and is well characterized by sporophyte features. *Grimmia triformis* can only be confused with *G. donniana*, from which it is nearly indistinguishable gametophytically. The most conspicuous difference is the included sporophytes of *G. triformis*; those of *G. donniana* are exserted. Other characters separating these species are the wider (70–100 μm), cribrate

peristome teeth and thick-walled exothecial cells of *G. triformis* versus the narrower (50–70 μm), entire peristome teeth and thin-walled exothecial cells of *G. donniana*. Some collections of *G. triformis* have been identified as *Coscinodon cribrus* (Hedw.) Spruce (Ignatov & Cao, 1994: 76), which also has included capsules, but the shape of the proximal laminar cells precludes any confusion.

Selected specimens examined (33). AUSTRIA. Salzburg: Rauriser Goldberg, Mielichhofer s.n. (BP-36855, p.p.). Tirol: Innervillgraten, "Kalchstein," Gander s.n. (BP-37549). FRANCE. Haute-Garonne: Port de Benasque, Pierrot s.n. (BCB-2578). ITALY. Vercelli: Alpes Penninae Pedemontii, in monte Tagliaferro, prope cacumen, 19 Aug. 1863, Carestia s.n. (JE). RUSSIA. Gorno Altayskaya Autonomous Oblast: Altai Mountains, Kobiguayuk Creek, Ignatov 0/474 (IBA-6997). SWITZERLAND. Bern: Fungfraujoeh am den "Hotelfelsen," Kol & Chorus s.n. (BP-80466, p.p.).

II. *Grimmia* (subg. *Orthogrimmia*) sect. *Montanae* I. Hagen, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1909(5): 16. 1909. TYPE: *Grimmia montana* Bruch & Schimp.

Autoicous or *dioicous*. Plants in compact tufts, seldom fragile, glaucous, green, olive-green, or brownish green above, blackish below. *Stems* to 1.5 cm tall, with central strand well developed, seldom with rhizoids the entire stem length; *axillary hairs* 3–8-celled, 50–175 μm long. *Leaves* erect and appressed or flexuous when dry, erect to spreading, sigmoid or straight, and flaccid or rigid when moist, 0.8–2.0 × 0.26–0.65 mm, narrowly ovate to ovate, acute to acuminate, keeled (occasionally weakly), plane or plicate; *margins* plane or partially recurved at the base; *costa* semi-terete, usually prominent on the dorsal surface, slightly to distinctly delimited; *lamina* 2–3(4)-stratose in the distal half, smooth; *distal cells* 4–20 μm, isodiametric, plane or bulging, smooth or papillose; *proximal paracostal cells* 10–55 × 7–20 μm, not hyaline, isodiametric to rectangular (1–6:1), the walls straight, the transverse walls thicker than the longitudinal walls; *proximal marginal cells* 9–50 × 6–20 μm, isodiametric to rectangular (1–5:1), with straight walls uniformly thickened or the transverse walls thicker than longitudinal walls; *hyaline hair-points* terete, straight, to 1.5 mm long, smooth or denticulate (serrate, with many acute teeth in some populations of *G. montana*). *Perichaetial leaves* 1.5–2.8(–4) × 0.5–0.9 mm, convolute and larger (2–3×) than vegetative leaves; *hyaline hair-points* terete, straight, to 1.5 mm, nearly smooth. *Androecia* axillary or terminal. *Setae* erect and straight or somewhat curved, 1–4.5 mm long. *Capsules* exserted, ovoid, ellipsoid or fusiform, symmetric (seldom slightly asymmetric

at base), smooth, stramineous to castaneous, with stomata at the urn base or lacking stomata; *exothelial cells* 16–70 × 10–55 μm, isodiametric to rectangular (1–4:1), thin- or thick-walled; *annulus* simple and persistent; *peristome teeth* 35–90 μm wide at the base, entire, split and cribrate or irregularly 2–3 cleft in the distal half, castaneous or orange, concolorous or contrasting in color with the urn; *opercula* conic, mammillate or rostrate; *calyptrae* cucullate. *Spores* 9–14 μm.

Distribution. All continents.

Grimmia subg. *Orthogrimmia* sect. *Montanae* is characterized by proximal marginal cells with the transverse walls thicker than the longitudinal walls, cucullate calyptrae, and a simple and persistent annulus.

4. *Grimmia alpestris* (Schleich. ex F. Weber & D. Mohr) Schleich., Cat. Pl. Helv. Ed. 2: 29. 1807 [1808]. *Grimmia alpestris* Schleich., Neues J. Bot. 1: 196. 1806 [1805], nom. inval. *Trichostomum pulvinatum* var. *alpestre* Schleich. ex F. Weber & D. Mohr, Bot. Taschenbuch 110. 1807. *Campylopus pulvinatus* var. *alpestris* (Schleich. ex F. Weber & D. Mohr) Brid., Muscol. recent. Suppl. 4: 75. 1819. *Dryptodon pulvinatus* var. *alpestris* (Schleich. ex F. Weber & D. Mohr) Brid., Bryol. Univ. 1: 198. 1826. *Grimmia donniana* var. *sudetica* Huebener, Muscol. Germ. 175. 1833, nom. illeg. incl. var. prior. *Grimmia donniana* var. *alpestris* (Schleich. ex F. Weber & D. Mohr) Hampe, Flora 20: 281. 1837. *Guembelia alpestris* (Schleich. ex F. Weber & D. Mohr) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. *Grimmia alpestris* var. *eualpestris* Loeske, Laubm. Eur. Part I: 101, figs. 25b, 27a–c. 1913, nom. inval. TYPE: [Switzerland, Valais:] In M[onte], Sylvio, *Schleicher s.n.* [Schleicher, Plantae cryptogamae Helveticae, n° 13] (lectotype, designated by Muñoz (1998), BM).

Grimmia holzingeri Cardot & Thér., in Holz., Bot. Gaz. 30: 123, tab. 11 fig. 2. 1900. *Grimmia alpestris* var. *holzingeri* (Cardot & Thér.) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 31, pl. 9. 1933. *Grimmia donniana* var. *holzingeri* (Cardot & Thér.) Wijk & Margad., Taxon 9: 190. 1960. TYPE: [U.S.A.] Montana: Flathead Co., vicinity of Lake McDonald, 4 mi. N of Belton, a station 30 mi. E of Kalispell, 6000–7000 ft., 25 July 1898. *Holzinger & Blake s.n.* (lectotype, here designated, PC; isoelectotypes, NY, PC).

Illustrations. Figure 8; Abramov and Abramova (1983: figs. 27, 9–12); Maier and Geissler (1995: fig. 24, sub *G. sudetica*).

Dioicous. Plants in compact tufts, glaucous or

green above and blackish below. *Stems* to 1.5 cm tall, with central strand well developed; *axillary hairs* 5–6-celled, 100–145 μm long. *Leaves* erect, appressed, and straight when dry, patent to spreading and somewhat flaccid when moist, 1–1.6 × 0.3–0.5 mm, ovate, acute, keeled, plicate, sometimes weakly so, plicae cells undifferentiated or more commonly longer and narrower than the other laminar cells; *margins* plane proximally and incurved at the apex; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2(–3)-stratose in the distal ½, smooth; *distal cells* 8–13 μm, isodiametric, bulging, smooth; *proximal paracostal cells* 10–35 × 8–20 μm, isodiametric to rectangular (1–3.5:1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; *proximal marginal cells* always with the transverse walls clearly thicker than the longitudinal walls, otherwise similar to the proximal paracostal cells; *hyaline hair-points* terete, straight, to 1 mm long, nearly smooth. *Perichaetial leaves* 2–2.5 × 0.75–0.9 mm, convolute and larger than vegetative leaves (2–3×); *hyaline hair-points* straight, to 1.5 mm, nearly smooth. *Androecia* terminal. *Setae* erect and straight, 2–4 mm long. *Capsules* exerted, mostly fusiform, seldom ovoid and then with a narrowed mouth, symmetric, smooth, castaneous, lacking stomata; *exothelial cells* 16–35 × 16–55 μm, isodiametric (1[2]:1), thick-walled; *annulus* simple and persistent; *peristome teeth* 50–70 μm wide at the base, entire or irregularly cleft in the apical part, brownish, concolorous with the urn; *opercula* conic or with a short and obtuse mammilla; *calyptrae* cucullate. *Spores* (9)10–13(–14) μm.

Diagnostic characters. (1) Lamina 2(–3)-stratose and plicate. (2) Cells always bulging. (3) Capsules mostly fusiform, castaneous, lacking stomata. (4) Exothelial cells ± isodiametric with thick walls.

Distribution (Fig. 9). Common in mountain chains in Europe and western North America, but known only from scattered localities in the intervening Asian areas. Mostly in open areas above the tree-line, between 1500 and 3400 m elevation on dry, exposed siliceous rocks. Mature sporophytes were present in 89.6% of the specimens studied.

Grimmia alpestris is somewhat variable. The amount of cuticular wax and consequent glaucous color vary according to habitat conditions. A greater amount of cuticular wax develops in dry and sunny habitats. The capsules are usually fusiform, but ovoid capsules are occasionally found.

Grimmia alpestris is easily distinguished from *G. reflexidens* when sporophytes are present. Diagnostic characters are the color and shape of the cap-

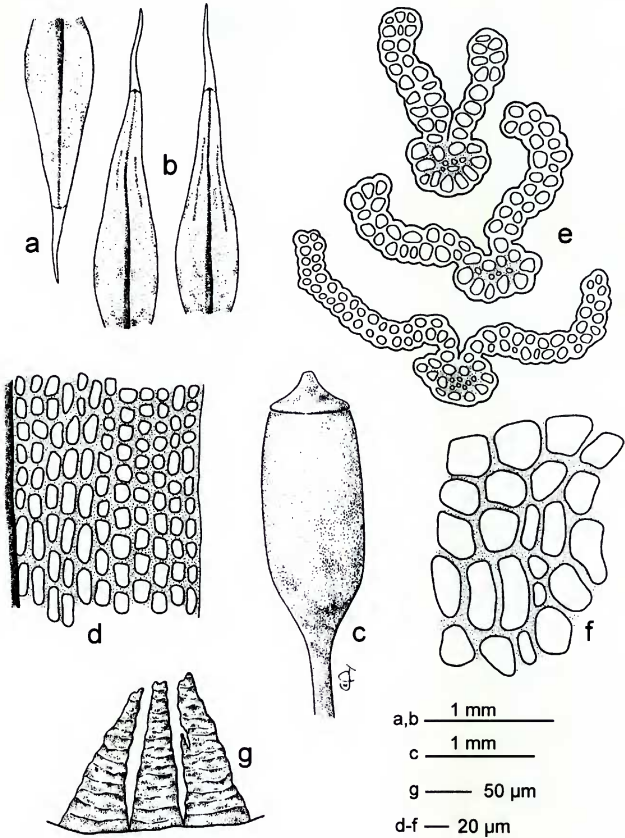


Figure 8. *Grimmia alpestris*. —a. Non-plicate leaf. —b. Plicate leaves. —c. Capsule. —d. Proximal leaf cells. —e. Transverse sections of leaf. —f. Medial exothelial cells. —g. Peristome teeth. [a, c, f, g, *Vajda s.n.* (BP-64281); b, d, e, *Schleicher s.n.* (JE).]

sules: brown and fusiform with the base attenuated into the seta in *G. alpestris* (Fig. 8c); stramineous and ovoid and abruptly connected with the seta in *G. reflexidens* (Fig. 16b). Dissecting capsules to study the shape of the exothelial cells and search for stomata may sometimes be necessary: *G. alpestris* has isodiametric, thick-walled exothelial cells

and lacks stomata, whereas the exothelial cells in *G. reflexidens* are rectangular and thin-walled, and 4–8 stomata can be found at the urn base.

On the other hand, sterile specimens can be difficult to name. When present, a diagnostic feature is the recurved margin of *G. reflexidens* (always plane in *G. alpestris*). The axillary hair-points are

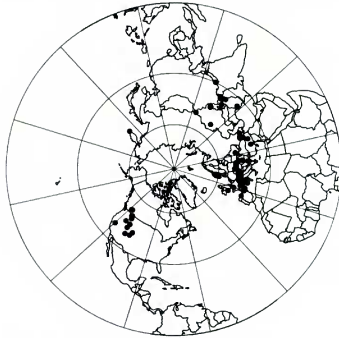


Figure 9. Distribution of *Grimmia alpestris*.

also useful: in *Grimmia alpestris*, they are 5–6-celled and 100–145 μm long, whereas in *G. reflexidens* they are 3–4(–5)-celled and 50–85 μm long.

Geissler and Maier (1995) and Maier and Geissler (1995) have employed the name *G. sudetica* Schwägr. for this taxon. This is an illegitimate name, however, as noted by Muñoz (1998).

Grimmia alpestris has a discontinuous circum-boreal distribution pattern. It has a western Europe–western North America disjunct distribution, and is not known from eastern North America or most of Asia. While this species is very likely absent from North America east of the Rocky Mountains, the lack of records from temperate Asian regions probably has more to do with undercollection. This species is typically associated with mountain chains: the Swiss Alps, the Fennoscandian Alps, the Balkans, the Carpathians s.l., and the Pyrenees in Europe, the Rocky Mountains in western North America, and the Altai, Caucasus, and Northwest-Himalayan chains in Asia. Bardunov (1974: 40) reported this species from the western Sayan Mountains (Russia, Krasnoyarsk Krai), but I was unable to obtain these specimens on loan.

Selected specimens examined (234). AFGHANISTAN. Panjskiri Valley, Ruka, *Köie* s.n. (IBA-4770). ANDORRA. Grau Roig, *Casas* s.n. (BCB-21724). AUSTRIA. **Carinthia**: Malniksee im Maltathal, *Breidler* s.n. (BP-6190). **Steiermark**: Hochalpe bei Turrach, 16 Aug. 1889, *Breidler* s.n. (FH). **Tirol**: Sulden (am Ortler), lower part of the Rosimtal, *Townsend* 92/522 (IBA-6279). BULGARIA. Rila planina, Mussalla, 2 Aug. 1908, *Podpěra* s.n. (TRH). CZECH REPUBLIC. Oester. Schlesien, Gesenke, Kessel, *Limpricht* s.n. (IBA-5468). FRANCE. **Alpes Maritimes**: S. Martin-Vésubie au Boréon, 28 July 1910, *Durand* s.n. (G). **Ariège**: près de l'étang d'Aron, Pozo d'Aula, 5 Sep.

1923, *Culmann* s.n. (Z). **Corsica**: montis Rotondo, supra "il Timozzo," 7 July 1880, *Lévrier* s.n. (TRH). **Hautes Alpes**: montie du Galibier du chemin à Lantiret, 26 Aug. 1926, *Culmann* s.n. (Z). **Isère**: La Lauvitel, 17 Aug. 1894, *Thériot* s.n. (TRH). **Normandie**: *Montagne* s.n. (RO). **Pyénées Centrales**: marginem lacus Lac de Gaube dicti, non longe a Caunterets, *Spruce* s.n. (NY, TCD). **Savoie**: Col de la Croix de Fer, *Cuynet* 22 (herb. Pierrot), GEORGIA. Gurschevi ad fontes fl. Dschandschachi Tschali, July 1877, *Brotherus* s.n. (H). Svanetia libera or. supra Chal-dechi et Kala, montis Djangau-tau, 8 Aug. 1890, *Sommier* & *Lévrier* s.n. (G). GERMANY. Kleinohans, *Anonymous* s.n. (TRH). ITALY. Mte. Lineone, *Balsamo-Crivelli* s.n. (RO); Ortler, Martelltal, Cevedalehütte, 30 July 1913, *Kern* s.n. (WRSL). KAZAKHSTAN. **Alma-Ata**: Chimbulak to Medeo Dam above Alma Ata, *Allen* 10798 (MO). **Kochketav**: Akmolinsk. distr. Athassar, montes Dshaksy-Arganaty, *Gordjagin* 198 (H-BR). NEPAL. NW Himalaya, *Troll* 67 (JE). NORWAY. **Christians**: Jotumheimen, Bukkelægret, 31 July 1879, *Bryhn* s.n. (TRH). **Sondre Trondhjems**: Opplad, Sliper, 19 May 1882, *Kawrin* s.n. (TRH); Valdres, Vang Skogstad, 8 Aug. 1889, *Bryhn* s.n. (TRH). PAKISTAN. **Hindukusch**: Tschitral, Bumboret-Tal, 1935, *Kerstan* s.n. (JE). **Kashmir**: Kalapani, Kamri Nala, Astor Valley, 10 July 1901, *Inayat-Khan* s.n. (H-BR). POLAND. Wysokie Tatry Mts. 1 km W of Czarny Staw tarn. 24 Aug. 1987, *Wójcicki* s.n. (IBA-7417, KRAM). ROMANIA. **Fogaras**: ad lacum Bulea, *Boros* s.n. (BP-112946). **Beszterce-Naszód**: Mt. Radnai havasok, montis Ünökő, ad Ünökői menedékház, *Felföldy* s.n. (BP-112943). RUSSIA. **Altayskaya Autononomus Oblast**: Altai, Stonovajatal in Katunjgebirge, 1 Aug. 1915, *Grand* s.n. (H-BR). **Kamchatka**: slope of Koshheva volcano, *Chernyadjeva* 16 (LE). **North Ossetia**: ad mare glaciale Zei, Aug. 1881, *Brotherus* s.n. (PC). SLOVAKIA. Siroka (Jaworiner-), *Chalubínski* s.n. (BP-36661); versus "Virágoskert" vallis Felkai-völgy, Velická dolina, *Boros* s.n. (BP-112912). SPAIN. **Gerona**: Circ de Concrós, *Lloret* s.n. (BCB-23455). **Huesca**: Benasc, La Renclusa, a l'ermita, *Casas* s.n. (BCB-27596). **Lérida**: Bof. Estany de Cavallers, *Casas* s.n. (BCB-39886). **Cantabria**: Peña Prieta, 14 Aug. 1987, *Muñoz* s.n. (IBA-606). SWITZERLAND. **Bern**: am Abhange des Piz Pischierwa, 21 July 1909, *Kern* s.n. (WRSL). **Rhaetia**: Davos, 20 Apr. 1890, *Amann* s.n. (TRH); Grand San Bernard, am Val Soren, 31 July 1895, *Bernet* s.n. (FH). **Graubünden**: Stätörhorn, 25 June 1888, *Adlerz* s.n. (TRH). **Wallis**: Südbabng des Santschpasses, 11 Aug. 1912, *Culmann* s.n. (FH). **Untere ngadin**: Zerneuz, Munt Baseglia, 16 July 1912, *Kern* s.n. (WRSL). TADZHIKISTAN. N slope of Darvazhski mountain range p. Zhingou, 19 July 1964, *Mamatkulor* s.n. (LE). TURKEY. **Artvin**: Ardanuc, Kordevan-dag (Yalniczam Deglari), at Küttül yayla, *Daris* & *Hedge* D.30403 (IBA-5098). **Kayseri**: Erçiyas-dagh, *Zederbauer* s.n. (W-2486). **Tunceli**: Kurdistan, Masgerth, 1881, *Brotherus* s.n. (H-BR). UKRAINE. Turka, oben Sta. Caterina, *Lorentz* s.n. (BP-36623). **Kirovograd**: Jabar-Syrt ad fontes fl. Vandam-czai, 23 Aug. 1900, *Alexeenko* s.n. (LE). UNITED KINGDOM. **Wales**: Carmarthenshire, near Marros, 29 Mar. 1907, *Knight* s.n. (FH).

CANADA. **British Columbia**: Revelstoke, 7 May 1890, *Macoun* s.n. (S). U.S.A. **Arizona**: Kaibab, *Mead* 990 (FH). **California**: Alpine Co., Monitor, *Lapham* s.n. (FH). **Colorado**: Larimer Co., Dream Lake, Rocky Mountain National Park, 1 Aug. 1929, *Braun* s.n. (MO). **Idaho**: Elmore Co., Atlanta, Boise National Forest, *Anonymous* s.n. (MO). **Montana**: Flathead Co., pr. Lake McDonald, 4

mi. N of Belton, a station 30 mi. E of Kalispell, 25 July 1898, *Holzinger & Blake s.n.* (TRH). **Utah:** San Juan Co., Elk Ridge, at Kigalia Ranger Sta., *Flowers 3633* (MO). **Wyoming:** Evanston, *Degener & Peiler 16928* (FH).

5. *Grimmia caespiticia* (Brid.) Jur., Laubm.-Fl. Oesterr.-Ung. 172. 1882. *Campylopus caespiticius* Brid., Muscol. Recent., Suppl. 4: 77. 1819 [1818]. *Grimmia funalis* var. *caespiticia* (Brid.) Hampe, Flora 20: 282. 1837. *Guembelia caespiticia* (Brid.) Müll. Hal., Syn. Musc. Frond. 1: 773. 1849. *Grimmia alpestris* var. *caespiticia* (Brid.) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 30. 1933. TYPE: [Switzerland. Bern:] St. Bernard, *Bridel s.n.* (holotype, B).

Grimmia sulcata Saut., Flora 24: 39. 1841. *Guembelia sulcata* (Saut.) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. TYPE: [Austria. Salzburg:] Pinzgauer Alpen, *Sauter s.n.* (lectotype, here designated, H-SOL; isolectotype, Z).

Grimmia jacquinii Garov. var. *subimberbis* Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 23: 552. 1866 [1867]. *Grimmia alpestris* var. *subimberbis* (Lindb.) Berggr., Kongl. Svenska Vetenskapsakad. Handl. 13(7): 49. 1875. *Grimmia caespiticia* var. *subimberbis* (Lindb.) Limpr., Laubm. Deutschl. 1: 780. 1889. *Grimmia sulcata* var. *subimberbis* (Lindb.) G. Roth, Eur. Laubm. 1: 431. 1903 [1904]. *Grimmia caespiticia* f. *subimberbis* (Lindb.) Podp., Consp. Musc. Eur. 283. 1954. TYPE: [Norway.] Spitsbergen: Amsterdam Island, 1861, *Holmgren s.n.* (lectotype, here designated, H-SOL).

Grimmia manniae Müll. Hal., Flora 70: 223. 1837. *Grimmia alpestris* var. *manniae* (Müll. Hal.) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 31. 1933. *Grimmia donniana* var. *manniae* (Müll. Hal.) Wijk & Margad., Taxon 9: 50. 1960. TYPE: [U.S.A.] California: Napa Soda Springs, 3 May 1886, *Mann s.n.* (lectotype, here designated, NY; isolectotype, PC).

Grimmia pyrenaica Kern, Jahreshber. Schles. Ges. Vaterl. Cult. 92: 38. 1915. TYPE: [Spain. Lérida:] Gavernie, auf eisenhaltigen Felsen dem Port de Boucharo, spanische Seite, 13 July 1914, *Kern s.n.* (lectotype, designated by Bednarek-Ochyra et al. (1992). WRSI; isolectotypes, BP-80423, KRAM, MA-8158, MA-10927).

Illustrations. Figure 10; Bednarek-Ochyra et al. (1992: fig. 1); Bruch et al. (1845: tab. 252, sub *G. sulcata*); Chałubiński (1882: tab. 9 fig. 16); Limpricht (1890: fig. 203); Maier and Geissler (1995: fig. 6); Nyholm (1956: fig. 69C).

Diocous. Plants in fragile tufts, glaucous or olive-green to blackish. Stems to 1 cm tall, with central strand well developed; axillary hairs 4-celled, 55–75 μm long. Leaves erect and appressed, and with incurved apices when dry, erect and rigid when moist, 0.8–1.8 \times 0.3–0.6 mm, ovate, acute, keeled, strongly plicate, the plicae of 2–5 rows of longer and more narrow cells with thicker walls; margins plane in the proximal half, incurved in the

distal half and cucullate at tip; costa semi-terete, prominent on the dorsal surface, clearly delimited; lamina 2(–3)-stratose in the distal half, smooth; distal cells 7–9 μm , isodiametric, bulging, usually papillose; proximal paracostal cells 14–35 \times 7–18 μm , isodiametric to rectangular (1–3:1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; proximal marginal cells 12–32 \times 10–14 μm , isodiametric to rectangular (1–3:1), with the transverse walls thicker than the longitudinal walls; hyaline hair-points terete, straight, to 0.4 mm long, smooth. Perichaetial leaves ca. 1.5 \times 0.4–0.5 mm, convolute and slightly larger than vegetative leaves; hyaline hair-points straight, to 0.5 mm, smooth. Androecia terminal. Setae erect and straight, 2.5–3.5 mm long. Capsules exerted, ovoid, symmetric, smooth, castaneous, with stomata at the urn base; exothecial cells 24–70 \times 10–28 μm , very irregularly isodiametric to rectangular (1–3:1), thin-walled; annulus simple and persistent; peristome teeth 35–50 μm wide at the base, \pm entire, brownish, concolorous with the urn; opercula mammillate or rostellate, and then with an oblique beak; calyptrae cucullate. Spores 10–14 μm .

Diagnostic characters. (1) Leaves with a strongly marked longitudinal plication on each side of costa. (2) Margin involute in the distal half and becoming cucullate at tip. (3) Hyaline hair-point very short, to 0.5 mm on the perichaetial leaves, but usually much shorter. (4) Laminar cells bulging. (5) Distal leaf cells usually papillose. (6) Capsules castaneous, with stomata at the base.

Distribution (Fig. 11). Europe, the Caucasus, Svalbard, and the west coast of North America; in open areas above the tree-line from 1000 and 2797 m elevation on dry, siliceous rocks. Mature sporophytes were present in 77% of the specimens studied.

Grimmia caespiticia is rather invariable in most respects, except glaucousness, which depends on the amount of wax deposited on the leaves. As in *G. alpestris*, this variation correlates with habitat conditions. The degree to which the cells bulge also varies. Usually they bulge prominently, but may be nearly smooth in some populations.

In fertile condition, the combination of plicate leaves, very short hair-points, and exerted capsules clearly distinguishes *G. caespiticia* from any other species in *Grimmia* or *Coscinodon*. Another useful character for separating this taxon from *G. alpestris* is the presence of stomata at the base of the capsule, absent in the latter species. In sterile condition, it is difficult (or at times impossible) to

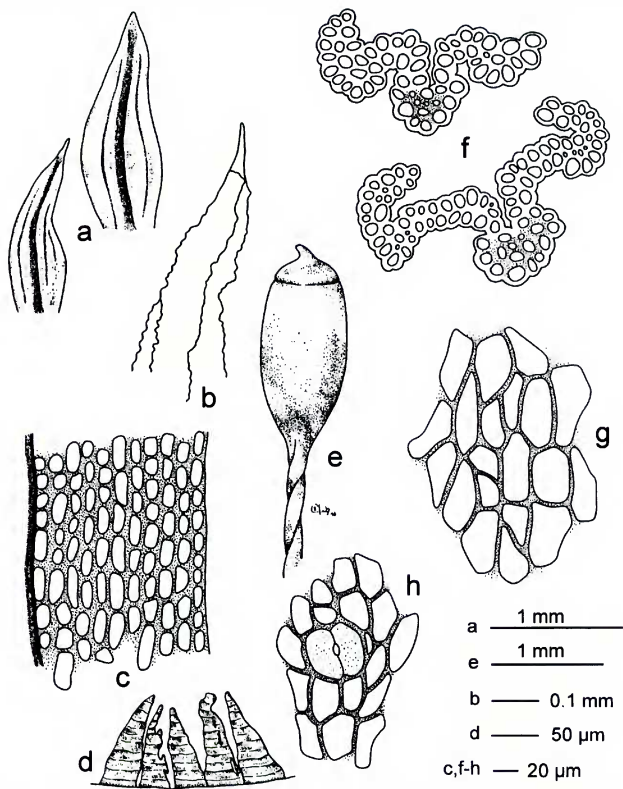


Figure 10. *Grimmia caespiticia*. —a. Leaves. —b. Dorsal view of papillose leaf apex. —c. Proximal leaf cells. —d. Peristome teeth. —e. Capsule. —f. Transverse sections of leaf with non-papillose cells. —g. Medial exothelial cells. —h. Proximal exothelial cells and stoma. [a, b, c, f, *Pierrot 201/100* (herb. Pierrot); d, e, g, h, *Rupidera 3* (SALA).]

separate this taxon from *Coscinodon cribrus*, a species also difficult to distinguish from *G. alpestris* and *G. reflexidens* when sterile. The differences alleged by previous authors (Cao & Vitt, 1986: 168; Nyholm, 1956: 151) are not reliable; the length of the proximal cells, the thickness of the cell walls, and the shape of the leaf apex vary inordinately in both taxa, as can be verified from fertile collections. The only useful character for separating sterile material of *G. caespiticia* and *C. cribrus* is the usually

papillose laminar cells in the former, as opposed to the always smooth laminar cells in the latter. This feature, though noted by Loeske (1913: fig. 32), has been neglected by later authors. Another useful character is the length and shape of the hair-points. *Grimmia caespiticia* has very short hair-points, never longer than 0.5 mm, which are always terete, even on the longest hairs. Hair-points in *Coscinodon cribrus*, however, are usually longer than 0.5 mm and flat below. From these differences, and af-

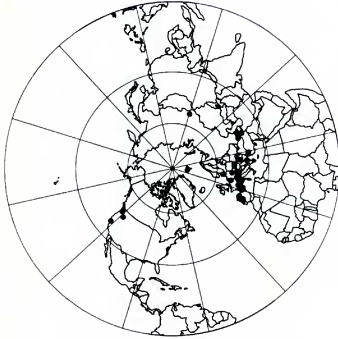


Figure 11. Distribution of *Grimmia caespiticia*.

ter studying the lectotype (H) and two isolectotypes (BM, PC) of *G. sinensianodon* Müll. Hal. (Müller, 1898: 188), I conclude that it is synonymous with *G. cribrerosus* (Hedw.) Spruce and not with *G. caespiticia* as proposed by Cao and Vitt (1986: 167). Those authors reported the type locality of *G. sinensianodon* to be the only known Chinese station for *G. caespiticia*. Because I have not found any specimens referable to *G. caespiticia* among the Chinese collections studied, this species must be excluded from the Chinese bryoflora.

The protologue of *Grimmia manniae* states "2 Majo 1886" as the collection date. The only two specimens I can find collected by Martha R. Mann in Soda Springs, the type locality, have "3 Majo 1886" as the collection date (NY, PC). Considering that they agree in every other respect with the protologue and that there are more typographical mistakes in the same paper (Müller, 1887), I have assumed that a mistake could have been made in transcribing the label in the original publication.

Selected specimens examined (163). ANDORRA. Tris-taina, *Casas s.n.* (BCB-10537). ARMENIA. Sisienskij rajon, s. Arevis, 5 July 1966, *Manakyan s.n.* (LE). AUSTRIA. Carinthia: Monte Caglians, auf dem Piz Ciadin, 8 July 1908, *Kern s.n.* (WRSL). Steiermark: Würslingen Höhe bei Stadl, 12 July 1878, *Breidler s.n.* (GOET). TIROL: Alpe Rossstal bei Innervillgraten, *Gander s.n.* (BP-36291). BELGIUM. Promenade Annette Lubin à Spa, Feb. 1906, *Cornet s.n.* (NY). BULGARIA. Mt. Pirin, decl. borealium mt. Mangar Tepe, *Simon s.n.* (BP-68488); Wichryn, ad viam Zwasticam, *Kuc s.n.* (BP-70237). FRANCE. Alpes-Maritimes: Saint-Dalmas-de-Tende, les Ciappe de Fontanalba, *Parriat s.n.* (BP-112934). Cantal: Plomb-du-Cantal, *Cuynet s.n.* (BP-112904). Hautes Alpes: plane nord du Combegnot, 21 July 1926, *P. Culmann s.n.* (Z). Isère: les Grandes Rousses, environs du lac Blanc, 20

Aug. 1894, *Thériot s.n.* (Z). Puy de Dôme: vallée du Chandeferer, 19 Aug. 1919, *Culmann s.n.* (Z). Pyrénées Centrales: Port de Bénasque, 12 Sep. 1845, *Spruce s.n.* (NY). GEORGIA. In jugo alpino inter flumina Neuskas et Skun pr. Svania occident. confine, *Sommier & Levier 364* (H). South Ossetia Autonomous Oblast: in alpe Zomorashch prope Ress ad fl. Terek, July 1881, *Brotherus s.n.* (H). GERMANY. Karl-Marx Stadt: Bärenstein (BP-112894). ITALY. Adamellogruppe, Leipziger Hütte, 27 July 1895, *Kern s.n.* (WRSL); Rizelembrai juxta Cól di Stelvio, *Lorentz s.n.* (BP-36283). NORWAY. Svalbard: Amsterdam Island, 1861, *Holmgren s.n.* (H-SOL). POLAND. Kozi-Wirch, den Gipfel, 3 Sep. 1876, *Chatubiński s.n.* (BP-36297). PORTUGAL. Beira Alta: Serra da Estrela, Cântaro Raso, pr. da vista para o Covao da Ametade, *Sérgio & Sêneca 8164* (IBA-5050). ROMANIA. Brasov: vallis Podragu, montes Fogarasi havasok, *Vajda s.n.* (BP-72021). RUSSIA. Irkutsk: Western Sayan, the river Ona in the upper part, *Bardunov s.n.* (NICH 306126). Stavropols'kij Kraj: Teberdinsky Reserve, 14 Sep. 1954, *Patrololova s.n.* (LE). SLOVAKIA. Tatra Magna, convallis "Sirkert" sub monte Lomnicki-csucs, *Boros s.n.* (BP-6188); Höher Rücken zwischen den Mengsdorfer und Koprovy-Spitze, *Chatubiński s.n.* (BP-36298); vallis Virágoskerl, supra lacu Felkaité, *Vajda s.n.* (BP-70417). SPAIN. Asturias: Somiedo, pr. El Puerto, La Vega de Peñueta, 4 Nov. 1995, *Muñoz s.n.* (IBA-6750). Ávila: bajada a la laguna de El Trampal, 9 Sep. 1995, *Muñoz s.n.* (IBA-6723). Cantabria: Peña Prieta, 14 Aug. 1987, *Muñoz s.n.* (BCB-25772). Gerona: Coma de l'Orri, *Lloret s.n.* (BCB-28890). Huesca: Benasc, La Renclusa, Ibón de Paderna, *Casas s.n.* (BCB-30444). Lérida: Areu, roques próximas al refugi, *Casas s.n.* (BCB-33173). Palencia: pico Curavacas, 12 July 1988, *Muñoz s.n.* (IBA-681). SWITZERLAND. Bern: Urbachtal bei der Gaulihütte, *Culmann s.n.* (MA 5870). Graubünden: Pischahorn im Fluelathal, *Amann BH-12* (Z). Valais: Distebalp, Saastal, *Amann BH-24* (Z). TURKEY. Bursa: Nordabhang des Ulu Dağ, *Walther 3318* (NY).

U.S.A. California: Napa, Soda Springs, 3 May 1886, *Mann s.n.* (NY). Oregon: Union Co., S shore of Antony Lake, Blue Mts., 17.5 mi. W of North Wood, *Hermann 28821* (C). Washington: Pierce County, Mt. Rainier Park, about 0.5 mi. from ranger station, *Lawton 4792* (MO).

6. *Grimmia montana* Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 128, tab. 250. 1845. *Guembelia montana* (Bruch & Schimp.) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. *Grimmia holmiensis* Lindb. ex Hartm., Handb. Skand. Fl. Ed. 7: 374. 1858, nom. inval. pro syn. TYPE: [Germany. Rhineland-Palatinate:] Donnersberg, Apr. 1843, *Gümbel s.n.* (lectotype, designated by Cao & Vitt (1986), BM).

Grimmia laxa Müll. Hal., Bot. Zeitung (Berlin) 5: 801. 1847. TYPE: Mexico. In monte Orizabae, *Deppe & Schiede s.n.* (lectotype, here designated, PC).

Grimmia fragilis Schimp., Syn. Musc. Eur. Ed. 2: 257. 1876, nom. illeg., non F. Weber, 1804. *Grimmia montana* var. *fragilis* (Schimp.) Loeske, Laubm. Eur. Part 1: 99. 1913. TYPE: [Portugal.] Ad rupes granit. in alpestribus Prov. Beira, Aug. 1848, *Welwitsch s.n.* (lectotype, here designated, BM).

Guembelia tenella Müll. Hal., Bot. Centralbl. 44: 388. 1890. *Grimmia tenella* (Müll. Hal.) Kindb., Enum. Bryin. Exot., Suppl. 2: 107. 1893. TYPE: [U.S.A.] Idaho: Coeur d'Alene, 6 Aug. 1888, Röll s.n. (lectotype, here designated, G; isoelectotypes, H-BR, JE, S).

Grimmia montana var. *longifolia* Cardot, in Gasilien, Rev. Bryol. 21: 24. 1893 [1894]. *Grimmia montana* f. *longifolia* (Cardot) Podp., Consp. Musc. Eur. 281. 1954. TYPE: [France. Puy de Dôme:] Auvergne, Pierre sur Haute, 1884, Gasilien s.n. (lectotype, here designated, TRH).

Grimmia montana var. *abnoba* H. Schmidt, Mitt. Bad. Landesvereins Naturk. Naturschutz Freiburg 2: 121, fig. 6. 1927. TYPE: [Germany. Württemberg:] Süd. Schwarzwald, südweste dem Schauinslandgipfel, Schmidt s.n. (lectotype, here designated, JE).

Grimmia montana f. *submutica* J. E. Zetterst. ex H. Möller, Ark. Bot. 26A(2): 31. 1933 [1934]. TYPE: [Sweden.] Juxta Husbyborg prope Upsaliam, 15 May 1855, Zetterstedt s.n. [Zetterstedt, Grimmiæ et Andreaeae exsiccatae, n° 21c] (lectotype, here designated, H-BR).

Illustrations. Figure 12; Bruch et al. (1845: tab. 250); Chahubiński (1882: tab. 8 fig. 14); Jóhannsson (1993: fig. 26); Maier and Geissler (1995: fig. 17); Nyholm (1956: fig. 69B).

Dioicous. Plants in flat or bulging cushions or tufts, olive-green at the tips, dark green or blackish below. Stems to 1 cm tall, with central strand well developed; axillary hairs 5–8-celled, 95–175 μm long. Leaves erect, loosely appressed and flexuous when dry, with patent proximal part and incurved apex, sigmoid in lateral view, rigid when moist, 1–2 \times 0.3–0.6 mm, abruptly acuminate from an ovate base, apex from somewhat to distinctly keeled, plane or with very weak plicae; margins plane proximally and incurved distally, forming a canaliculate apex; costa semi-terete, prominent on the dorsal surface, slightly to distinctly delimited; lamina 2(3–4)-stratose in the distal half, smooth; distal cells 4–8 μm , isodiametric, plane or slightly bulging on the dorsal surface, smooth; proximal paracostal cells 20–50 \times 8–15 μm , rectangular (2–4.5: 1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls; proximal marginal cells 20–50 \times 8–15 μm , rectangular (2–4.5: 1), with the transverse walls thicker than the longitudinal walls; hyaline hair-points terete, straight, to 1.5 mm long, obtusely denticulate (rarely serrate). Perichaetial leaves 1.7–2.4(–4) \times 0.6–0.9 mm, convolute and larger than vegetative leaves (2 \times), yellowish at the base; hyaline hair-points similar to those of vegetative leaves. Androecia terminal. Setae erect and straight, 2–4 mm long. Capsules exserted, ovoid or ellipsoid, symmetric (seldom slightly asymmetric at base), smooth, castaneous, lacking stomata; exothecial cells 30–70 \times

10–25 μm , rectangular (2–4: 1), thin-walled; annulus simple and persistent; peristome teeth 50–90 μm wide at the base, irregularly split and perforate, \pm cribrate, castaneous, concolorous with the urn; opercula rostrate, the beak oblique; calyptrae cucullate. Spores 10–14 μm .

Diagnostic characters. (1) Leaves flexuous, sigmoid in lateral view when moist, ending in a long acuminate apex. (2) Laminar cells not bulging. (3) Plants dioicous. (4) Capsules lacking stomata. (5) Opercula rostrate with oblique beak.

Distribution (Fig. 13). Western Europe, the Canary Islands, Greenland, and North America; coniferous and broad-leaved formations, and also open areas, mostly below the tree-line, between 300 and 2000 m elevation on dry, siliceous rocks. Mature sporophytes were present in 69% of the specimens studied.

Grimmia montana is a rather stenotypic taxon throughout its entire distribution range. Some minor gametophytic differences between North American and Eurasian specimens may be observed, but the sporophytes are identical worldwide. Eurasian populations from lower latitudes and/or elevations have longer and more acuminate leaves than those from higher latitudes and/or elevations. North American populations resemble northern Eurasian populations in having leaves with a short leaf acumen. In very exposed places at high altitudes, cells bulge slightly at the dorsal laminar surface, and the acumina are shorter. Male plants are shorter and have leaves with shorter hair-points, sometimes muticous. They are easy to recognize because their stems end in globose perigonia.

Circumboreal but scattered, *Grimmia montana* is the only species of subgenus *Orthogrimmia* known from Greenland and Baffin Island. Oddly, there are no collections from continental eastern North America; all material from that region so identified actually represents *G. incurva* with erect and straight setae. Brodo and Alstrup (1981: 231–233) documented the same distribution pattern for two lichens, *Bryoria subdivergens* (Dahl) Brodo & D. Hawksw. and *Rhizocarpon bolanderi* (Tuck.) Herre, and noted that such a pattern is unknown in other plant groups. Subsequently, Blom (1996: fig. 46) illustrated the same pattern for *Schistidium umbrosum* (J. E. Zetterst.) H. H. Blom (Musci, Grimmiaceae).

Grimmia montana was recorded from China and Tibet by Cao and Vitt (1986: 161–164, fig. 19), but all specimens listed by those authors represent other species, mainly *G. longirostris*; hence *G. montana* can be deleted from the Chinese bryoflora.

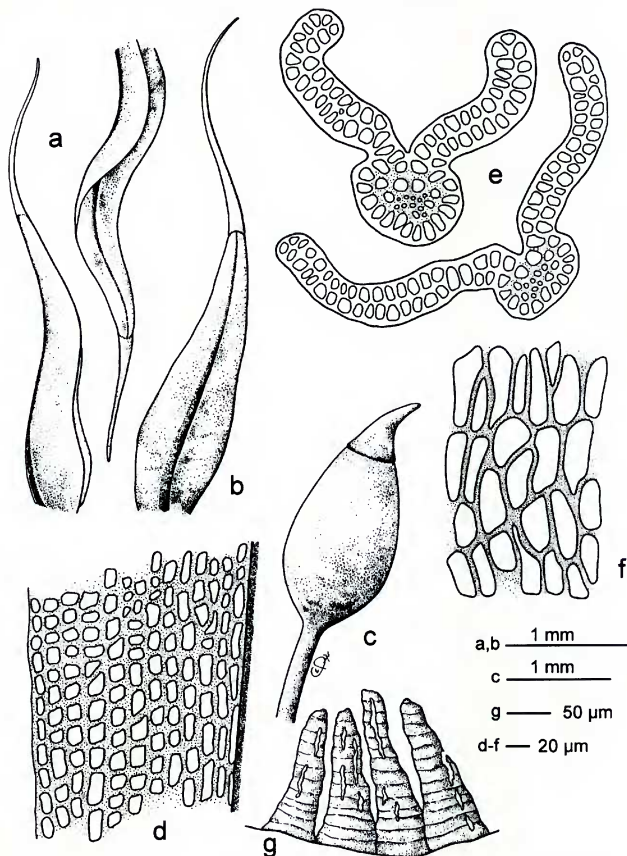
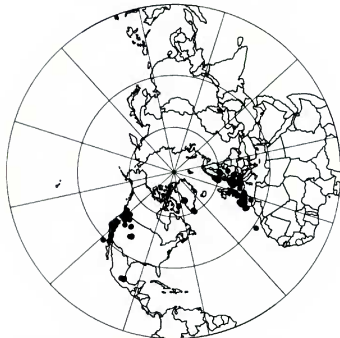


Figure 12. *Grimmia montana*. —a, b. Leaves. —c. Capsule. —d. Proximal leaf cells. —e. Transverse sections of leaf. —f. Medial exothecial cells. —g. Peristome teeth. [a, *Gasilien* s.n. (TRH); b, d, e, *Gümbel* s.n. (BM); c, f, g, *Kaurin* s.n. (TRH).]

Cao and Vitt (1986: 161) also synonymized *G. brachyphylla* Cardot with *G. montana*, based on several character states shared by these two species. Nevertheless, the features listed by these authors are common to many other species in the genus, and thus inconclusive. Based on a study of the

types, I conclude that *G. brachyphylla*³ is synonymous with *Coscinodon humilis* Milde.

³ TYPE: South Korea, Pomasa, 800 m, 1906, *Faurie 218* (lectotype, here designated, PC; isolectotypes H, H-BR, NY).

Figure 13. Distribution of *Grimmia montana*.

Grimmia montana has been also reported from the Russian Far East (Afonina, 1986: 223, ris. 2 figs. 1–8; Ignatov & Afonina, 1992: 42); however, all the specimens supporting these reports are *G. longirostris* or *G. reflexidens*.

Selected specimens examined (294). ANDORRA. Tristaina, Casas s.n. (BCB-10536). AUSTRIA. **Niederosterreich:** Arndorf, 19 Aug. 1894, Baumgartner s.n. (TRH). **Tirol:** Zaithal, Sölden, Dixon & Nicholson s.n. (BP-80258). BELGIUM. Ardennas, Cardot s.n. (FH); Montagn-russes bei Spa, Cornet s.n. (BP-36286). FRANCE. **Maine-et-Loire:** Angers, 10 Apr. 1857, Perraudière s.n. (G). **Calvados:** Condé-sur-Noireau, Husnot s.n. (FH). **Pyrénées Centrales:** Pic du Midi, Aug. 1847, Philippi s.n. (FH). **Savoie:** pr. Chamonix, loco dicto Pierre à Bérard, Payot s.n. (TRH). **Vosges:** Reinsch s.n. (FH). GERMANY. **Baden-Württemberg:** circa Heidelbergam, Braun s.n. (FH). **North Rhine-Westphalia:** Bertram s.n. (IBA-4125). ITALY. Adamellogruppe, Val di Genova, 28 July 1895, Kern s.n. (WRSL). NORWAY. **Oppland:** Dovre, Vaarstien ad viam publ. pr. Nestadsvallas, Kaurin s.n. (TRH). **Oslo:** montis Egeberg, 18 June 1870, Zetterstedt & Wickboom s.n. (TCD). **Sor Trondelag:** Oppdal, Sliper, 1 July 1883, Hagen s.n. (TRH). POLAND. Sudetes Mts., Karkonosze Range, Sniezny Kociol, July 1876, Limpricht s.n. (FH). PORTUGAL. **Beira Alta:** Serra d'Estrela, in jugis alpinis editionibus, 31 July 1878, Lenier s.n. (G). **Beira Baixa:** Sabugal, a 2 km de Quadrazais, ponte do rio Côa, Sérgio s.n. (IBA-4506). **Douro Litoral:** na cima do Serra do Marao, Ervideira s.n. (LISU-P53901). **Minho:** Serra de Peneda-Gerêz, Soajo, Branda da Bouça dos Homens, Sérgio & Sim-Sim s.n. (LISU-154131). **Trás-os-Montes:** Pitoões das Júnias, Montalegre, Sérgio & Schumacker s.n. (LISU-154132). SPAIN. **Almería:** Sierra de los Filabres, barranco de la Verruga, 26 May 1990, García-Zamora & Ros s.n. (MUB). **Asturias:** Puerto de Leitariegos, 15 July 1835, Durieu s.n. (PC). **Ávila:** bajada a las lagunas de El Trampal, 9 Sep. 1995, Muñoz s.n. (IBA-6722). **Burgos:** roquedo de Carramata, Heras s.n. (VIT 1050/84). **Cantabria:** Puertos de Riofrio, 12 July

1988, Muñoz s.n. (IBA-618). **Cáceres:** Acebo, Cros & Brugués s.n. (BCB-21766). **Gerona:** torrent de la Llosa, Lloret s.n. (BCB-23440). **Granada:** Sierra Nevada, San Gerónimo, Casares Gil s.n. (MA 8155). **Huesca:** lago de Urdiceto, Casas s.n. (IBA-3984). **Lérida:** Alta Ribagorça, marge esquerre de la Noguera Ribagorçana, Canalis s.n. (BCC-1278). **León:** Ancares, subiendo al Cuffia, Cros & Lloret s.n. (BCB-20118). **La Rioja:** Posadas, Sierra de la Demanda, Casas s.n. (BCB-2472). **Madrid:** Puerto de Navacerrada, Casares Gil s.n. (MA 8156). **Navarra:** monte Mendaur, Arraiza s.n. (NAU-3284). **Orense:** pr. Casayo, Fonte da Cova, Aedo s.n. (IBA-3177). **Palencia:** Valdecebollas, Aedo s.n. (IBA-3933). **Salamanca:** Alto de Los Lobos, subiendo a la Peña de Francia, 26 Sep. 1991, Muñoz s.n. (IBA-3595). **Tenerife:** Cañadas del Teide, Apr. 1906, Pitard s.n. (MO). **Zamora:** San Pedro de las Herrias, Rupidera 52 (SALA). SWEDEN. Mt. Huddinges, 2 June 1902, Arvén s.n. (FH); Norrkåping, 1878, Olsson s.n. (TRH); Stockholm, Lidingo, 30 Apr. 1859, Zetterstedt s.n. (TRH); Uppsala, Bårby, 14 June 1859, Zetterstedt s.n. (TRH). SWITZERLAND. [No locality given.] 1842, Anonymous s.n. (BM). UNITED KINGDOM. **England:** Somerseset, near Highbidge, 24 Mar. 1913, Nicholson s.n. (FH).

CANADA. **British Columbia:** Sproats Landing, 20 June 1890, Macoun s.n. (S). **Northwest Territories:** Cumberland peninsula, Anonymous s.n. (NY). GREENLAND. Groenlandia boreal, Clausshavn, 1870, Berggren s.n. (TRH); SW Greenland, Narssaq, on Narssaqund at Gronlands Geologiske Undersogelser camp and general vicinity, Steere 62-982 (NY). MEXICO. **Baja California:** National Park, San Pedro Mártir Mts., Hammond 10837 (NY). Guadalupe Island, summit, Moran 5664 (FH). **México:** Popocatepetl, Sharp 4749 (TENN). **Puebla:** S slope of Ixtacehuatl, Vitt 17520 (TENN). **Veracruz:** Monte Orizaba, Purpus 4277 (PC). U.S.A. **California:** San Bernardino Co., W face of Cucamonga Mt., Sweet Jr. 189 (FH). **Colorado:** Eagle Co., 1 mi. W of Wolcott, Weber B-15354 (MO). **Idaho:** Elmore Co., Hot Springs, Atlanta, Berse National Forest, MacFadden 18766 (FH). **Montana:** Mineral Co., shore of Clark Fork, Rest Area on US 10, 3 mi. W of Alberton, Hermann 22562 (FH). **Nevada:** Kings Canyon near Carson, 2 June 1902, Baker s.n. (PC). **Oregon:** Multnomah Co., Larch Mountain near summit, Redjean 11541 (MO). **Washington:** Spokane, 11 May 1909, Bonser s.n. (FH). **Wyoming:** Yellowstone, 2 Sep. 1888, Roll s.n. (JE).

7. *Grimmia nivalis* Kindb., in Macoun, Bull. Torrey Bot. Club 17: 271. 1890. TYPE: [Canada.] British Columbia: Gold Range, 7000 ft., 10 Aug 1889, Macoun s.n. (lectotype, here designated, S; isolectotypes, CANM-198090, H-BR).

Grimmia papillinervis Kindb., Rev. Bryol. 34: 89. 1907. TYPE: Canada. British Columbia: Skagit summit, 18 July 1905, Macoun s.n. (holotype, S).

Illustrations. Figure 14; Allen (1995: figs. 3–5).

Dioicous. Plants in tufts, olive-green. Stems to 1.5 cm tall, with central strand weakly developed; axillary hairs 5–7-celled, ca. 130 μ m long. Leaves erect and appressed when dry, patent, rigid when moist, 1.1–1.8 \times 0.3–0.5 mm, ovate, acute, strong-

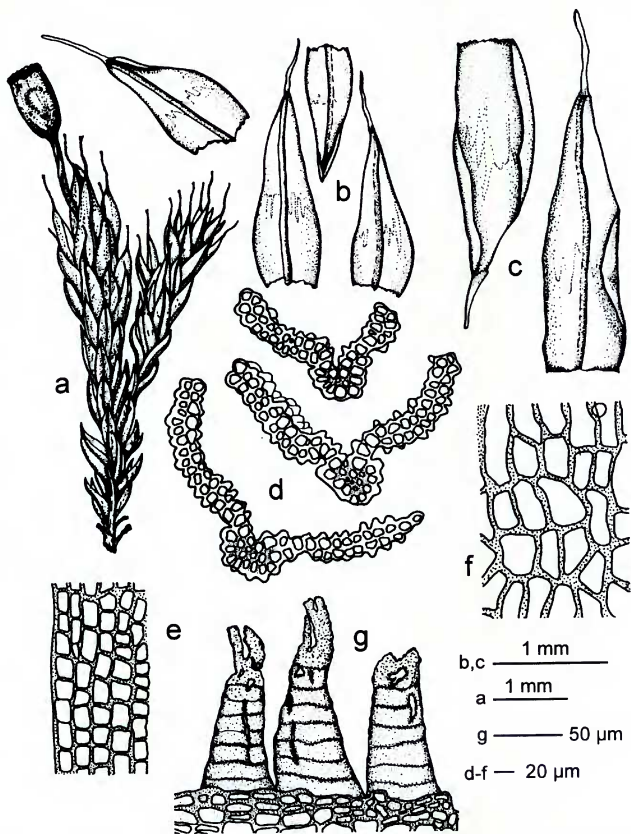


Figure 14. *Grimmia nivalis*. —a. Habit. —b. Leaves. —c. Perichaetial leaves. —d. Transverse sections of leaf. —e. Proximal leaf cells. —f. Medial exothelial cells. —g. Peristome teeth. [Howell s.n. (FH).]

ly keeled, plane or weakly plicate; *margins* plane proximally and incurved distally; *costa* semi-terete, prominent on the dorsal surface, clearly delimited; *lamina* 2-stratose in the distal half, smooth; *distal cells* 6–9(–11) μm , isodiametric, bulging, papillose; *proximal paracostal cells* 17–35 \times 15 μm , isodiametric to rectangular (1–2:1), the walls straight, uniformly thickened or the transverse walls thicker

than the longitudinal walls; *proximal marginal cells* 9–14 \times 9–11 μm , isodiametric to rectangular (1–1.5:1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.5 mm long, smooth. *Perichaetial leaves* 1.7–2.8 \times 0.6–0.9 mm, convolute and larger than vegetative leaves (2 \times); *hyaline hair-points* straight, to 0.75 mm, smooth. *Androecia* not seen. *Setae* erect

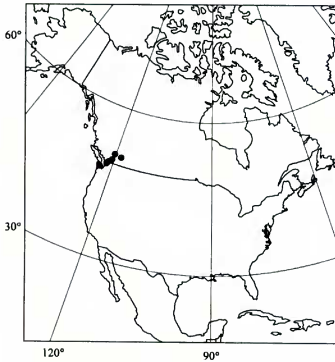


Figure 15. Distribution of *Grimmia nivalis*.

and straight, ca. 3 mm long. Capsules exerted, ovoid, symmetric, smooth, castaneous, with stomata at the urn base; exothecial cells $28\text{--}55 \times 10\text{--}35 \mu\text{m}$, rectangular or (seldom) isodiametric (1.4–4: 1), thick-walled; annulus simple and persistent; peristome teeth $55\text{--}80 \mu\text{m}$ wide at the base, split in 2–3 branches in the distal $\frac{1}{2}\text{--}\frac{1}{2}$, castaneous, concolorous with the urn; opercula conic, mammillate or short-rostellate, and then the beak oblique; calyptrae cucullate. Spores $9\text{--}14 \mu\text{m}$.

Diagnostic characters. (1) Lamina plane or weakly plicate. (2) Cells bulging and papillose. (3) Plants dioicous. (4) Capsules castaneous with stomata at the base.

Distribution (Fig. 15). Known only from the northwestern United States (Washington) and western Canada (British Columbia); open areas between 620 and 2100 m elevation on siliceous, seemingly dry rocks. Mature sporophytes were present in 94% of the studied specimens.

Both *Grimmia nivalis* and *G. alpestris* have ovate, somewhat glaucous leaves, long hair-points and bulging laminar cells, and their overall macroscopic aspect is quite similar. Nevertheless, microscopic examination distinguishes both species at once: transverse leaf sections of *G. nivalis* reveal scattered thick papillae on the lamina, and stomata on the capsules. Leaf cells of *G. alpestris* are bulging but not papillose, and capsules of this species lack stomata. Moreover, capsules of *G. alpestris* are mostly fusiform in shape, whereas those of *G. nivalis* are ovoid. *Grimmia caespiticia*, the only other species in subgenus *Orthogrimmia* with papillose

laminar cells and stomata on the capsule, usually has very short hair-points and strong plicae along both sides of the costa.

Allen (1995: 162–164) considered *Grimmia nivalis* synonymous with *G. tenerrima* Renaud & Cardot (*G. reflexidens* in the sense of this paper). Both species are macroscopically similar, but they can be separated because *G. nivalis* is a dioicous species with papillose cells and castaneous capsules, whereas *G. reflexidens* is autoicous, never has papillose cells, and the capsules are stramineous.

Specimens examined (13). CANADA. **British Columbia:** Gold Range, 10 Aug. 1889, *Macoun s.n.* (CANM-198089, CANM-198090, H-BR, NY [4 replicates], S); Summit Lake, 18 July 1905, *Macoun s.n.* (CANM-135430); Skagit summit, 18 July 1905, *Macoun s.n.* (S); Spence's Bridge, 28 May 1889, *Macoun s.n.* (PC). U.S.A. **Washington:** Mt. Baker, 15 July 1931, *Howell s.n.* (FH); Clallam Co., Mt. Angeles, 23 July 1931, *Howell s.n.* (FH).

8. *Grimmia reflexidens* Müll. Hal., Syn. Musc.

Frond. 1: 795. 1849. TYPE: Chile. *Pöppig s.n.* (lectotype, here designated, BM; isolectotypes, JE, NY, PC).

Grimmia subsulcata Limpr., Laubm. Deutschl. 1: 757. 1889. *Grimmia sessitana* var. *subsulcata* (Limpr.) Breidl., Mitt. Naturwiss. Vereines Steiermark 23: 88. 1892 [1891]. *Grimmia alpestris* subsp. *subsulcata* (Limpr.) Kindb., Eur. N. Amer. Bryin. 2: 221. 1898. *Grimmia alpestris* f. *subsulcata* (Limpr.) Loeske, Laubm. Eur. Part I: 104. 1913. *Grimmia alpestris* var. *subsulcata* (Limpr.) Broth., in Engl., Nat. Pflanzenfam. Ed. 2, 10: 309. 1924. *Grimmia sessitana* f. *subsulcata* (Limpr.) Loeske, Biblioth. Bot. 101: 117. 1930. TYPE: [Austria.] Steiermark: auf Glimmerschiefer "Speiereben bei Schoder," 9 Aug. 1883, *Breidler s.n.* (holotype, BP).

Guembelia lamellosa Müll. Hal., Bot. Zeitung (Berlin) 12: 318. 1854. *Grimmia lamellosa* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1872/73: 72. 1874. TYPE: [France, Haute Garonne:] in Pyrenaeis centralibus, ad lacum Espingo (lectotype, designated by Deguchi (1978), PC; isolectotype, H-SOL).

Grimmia sessitana De Not., Atti Reale Univ. Genova 1: 704. 1869. *Grimmia exannulata* Lindb. ex Broth., Acta Soc. Sci. Fenn. 19(12): 87. 1892, nom. inval. *Grimmia alpestris* var. *stomata* Loeske, Laubm. Eur. Part I: 104 figs. 26c, f, g, 27d, e, i, k. 1913, nom. illeg. *Grimmia alpestris* var. *sessitana* (De Not.) I. Hagen, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1909(5): 22. 1909. *Grimmia alpestris* f. *sessitana* (De Not.) Loeske, Laubm. Eur. Part I: 104. 1913. TYPE: [Italy, Vercelli:] Frane alle scaturigini del Vogna, sotto l'ospizio della Valdobbia in Val Sessia, *Carestia s.n.* (lectotype, designated by Cao & Vitt (1986), RO; isolectotypes, BM [2 replicates], FH, WRSU).

Grimmia anceps Boulay, Musc. France 1: 371. 1884. TYPE: [France, Haute-Savoie:] Col de Berard a d'Anchane-Mt. Blanc, *Pavot s.n.* (lectotype, here designated, PC; isolectotype, BP-36692).

- Grimmia tenerima* Renaud & Cardot, Bot. Gaz. 15: 40, pl. 6 A. 1890. TYPE: [U.S.A.] Oregon: Mt. Hood, Henderson 1239 (lectotype, here designated, PC; isoelectotype, NY).
- Grimmia grisea* Cardot, Bull. Herb. Boissier sér. 2, 6: 7. 1906. TYPE: South Georgia, Cumberland Bay, Skottsberg 307 (holotype, PC? not found; isotypes, H-BR, S).
- Grimmia subpapillinervis* Kindb., Rev. Bryol. 36: 98. 1909. TYPE: [Canada,] British Columbia: Ambean Valley, 10 July 1908, Brinkman s.n. (lectotype, here designated, CANM-198100).
- Grimmia subcaespiticia* Schiffn., Ann. K. K. Naturhist. Hofmus. 27: 490. 1913. TYPE: [Turkey, Malatya,] Kurdistania occidentalis, Taurus Cataonicus, in convalibus subalpinis prope vicum Bekikara inter urbem Malatja et vicum Kjahta, ca. 1600 m, 18 July 1910, Handel-Mazzetti s.n. (lectotype, here designated, FH; isoelectotype, H-BR).
- Grimmia asperitricha* Dixon & Sainsbury, Trans. & Proc. Roy. Soc. New Zealand 75: 173. 1945. TYPE: New Zealand, South Island: Tasman Glacier, near De La Beche Hut, Sainsbury 756 (lectotype, here designated, BM; syntypes, BM [Sainsbury 753, 757, 771, 772, 799]).
- Grimmia alpestris* f. *hybrida* Chal., Pamietn. Fyzyogr. 2: 63. 1882. *Grimmia alpestris* var. *hybrida* (Chal.) Chal. Enum. Musc. Frond. Tatr. 56. 1886. *Grimmia sessitana* f. *longifolia* Loeske, Biblioth. Bot. 101: 116. 1930, nom. illeg. incl. f. prior. TYPE: [Slovakia,] Tatra, Polnischer-Kaum, v.d. Felkaer-Thal, 27 Aug. 1879, Chalubiński s.n. (lectotype, here designated, BP-36703).
- Grimmia donniana* f. *antarctica* Kuc, Rev. Bryol. Lichenol. 36: 659, figs. 1, 2, 3d, e, 4, 5. 1969. TYPE: Antarctica, Queen Mary Land: Bunge Hills, in the neighbourhood of the Polish Base, 25 June 1959, Rózycki s.n. (holotype, KRAM; isotype, IBA-7386).

Illustrations. Figure 16; Cao and Vitt (1986: fig. 20a, c, e-l, n, p, q, s, u; Deguchi (1978: fig. 41, sub *G. subsulcata*); Maier and Geissler (1995: fig. 23, sub *G. sessitana*).

Autoicous. Plants in tufts, yellowish green at the tips, brownish green, brown, or blackish below. **Stems** ca. 1 cm tall, occasionally with rhizoids throughout, with central strand well developed; **axillary hairs** 3–4(5)-celled, 50–85(–100) μm long. **Leaves** erect and appressed when dry, patent to spreading and rigid to somewhat flaccid when moist, 1–1.8 \times 0.25–0.45 mm, ovate to narrowly ovate, acute, keeled, plane or very weakly plicate; **margins** plane or recurved to $\frac{1}{2}$ the leaf length on one side and proximally on the other side, occasionally only briefly and narrowly recurved proximally on one side; **costa** semi-terete, prominent on the dorsal surface, clearly delimited; **lamina** 2-stratose in the distal half, smooth; **distal cells** 8–12 μm , isodiametric, plane or bulging, smooth; **proximal paracostal cells** 20–55 \times 8–10 μm , rectangular (2–6:1), the walls straight, uniformly thickened or the transverse walls thicker than the longitudinal walls;

proximal marginal cells 20–50 \times 8–13 μm , rectangular (2–5:1), with the transverse walls thicker than the longitudinal walls; **hyaline hair-points** terete, straight, to 0.5 mm long, smooth or very weakly denticulate. **Perichaetial leaves** 1.8–2.7 \times 0.5–0.85 mm, convolute and larger than vegetative leaves (2 \times); **hyaline hair-points** terete or somewhat flattened proximally in longer hair-points, straight, to 1.5 mm, nearly smooth. **Androecia** axillary or terminal. **Setae** erect and straight, 1.5–3 mm long. **Capsules** exerted, ovoid or ellipsoid, symmetric (rarely slightly asymmetric at the base), smooth, stramineous, with stomata at the urn base; **exothelial cells** 35–70 \times 10–35 μm , irregularly rectangular (1.5–3:1), thin-walled; **annulus** simple and persistent; **peristome teeth** 45–70 μm wide at the base, entire or split, orange, contrasting in color with the urn; **opercula** conic, obtuse or mammillate; **calyptrae** cucullate. **Spores** 10–14 μm .

Diagnostic characters. (1) Axillary hairs 3–4(5)-celled, 50–85(–100) μm long. (2) Proximal cells mainly rectangular, 2–5:1. (3) Capsules stramineous, with stomata at the base. (4) Exothelial cells rectangular, with thin walls.

Distribution (Fig. 17). Known from all continents; woody formations and open areas from 850 to 3500 m, except in Antarctica and surrounding islands, where it grows at sea level. It prefers damp or moistened habitats close to rivulets and snowbeds, and is not uncommon in shaded places. Within section *Montanae*, this species is the least xerophilous member, even growing on rocks that are periodically flooded, mainly from spring thaw. Mature sporophytes were present in 82% of the studied specimens.

Grimmia reflexidens is a widely distributed and gametophytically variable species, and identification of sterile specimens can be impossible. Plants growing in drier and more sunny habitats were described in Europe as *G. subsulcata*. They have shorter and more ovate leaves with (usually) strongly bulging cells, and can also have weak longitudinal plicae. On the other hand, plants from exceedingly moist places have more flaccid leaves and a high number of rhizoids, and are closer to the traditional concept of *G. sessitana*. This distinction of these two taxa is untenable, as the correlation between the observed characters is not absolute. Plants with very long proximal paracostal cells and recurved margins, typical of the *G. sessitana* concept, can exhibit strongly bulging cells, and do not differ from other material in sporophytic features.

The leaf margins of *G. reflexidens* are usually

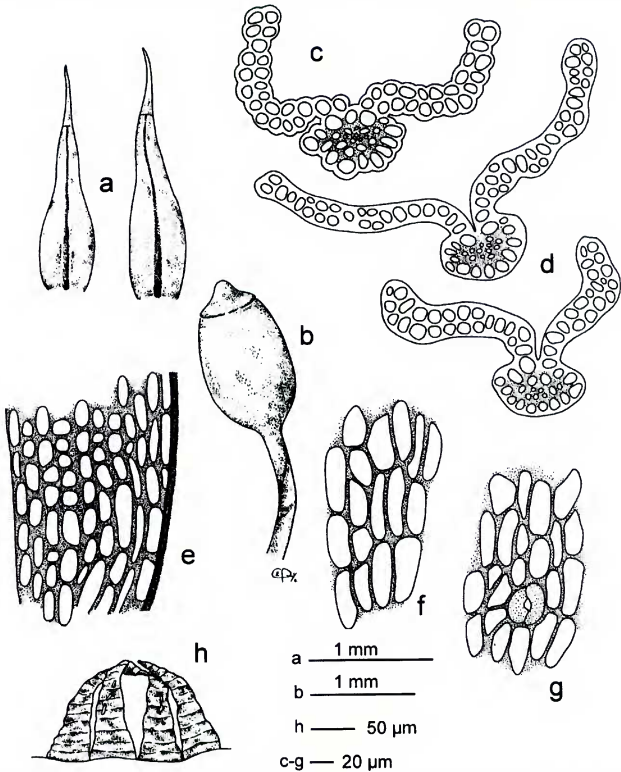


Figure 16. *Grimmia reflexidens*. —a. Leaves. —b. Capsule. —c. Transverse section of leaf with bulging cells. —d. Transverse sections of leaf with smooth cells. —e. Proximal leaf cells. —f. Medial exothelial cells. —g. Proximal exothelial cells and stoma. —h. Peristome teeth. [a, b, e-h, *Carestia s.n.* (PAV); c, *Brinkman s.n.* (CANM-198100); d, *Breidler s.n.* (BP-26598).]

plane in the proximal half. However, some populations have the margins recurved for part of their length, a feature that has been considered stable and of prime taxonomic value, causing many misidentifications.

Grimmia reflexidens was originally described as dioicous, because the perigonia and perichaetia usually occur at the ends of separate branches and so the autoicous condition can be extremely difficult to demonstrate. The sporophyte is rather sten-

otypic, and when fresh is easy to recognize with a 16–20 \times hand lens. The combination of straight setae and usually stramineous urns crowned with a distinct orange peristome is diagnostic and makes it unnecessary to dissect capsules to observe stomata. Populations with old capsules, already brown and damaged, are more problematic. In such cases, capsule color can be the same as in *G. alpestris*. The only sporophytic characters that vary to some degree are the orientation of the setae and the

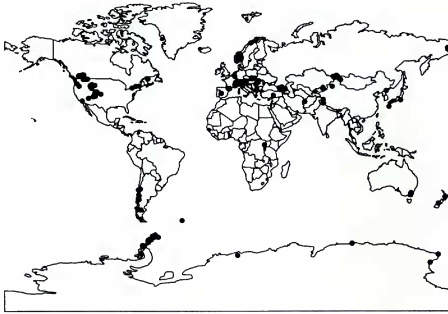


Figure 17. Distribution of *Grimmia reflexidens*.

shape of the opercula. The setae can be straight or weakly inclined, even in the same population. The operculum can be conic and obtuse, or mammillate. Both characters vary randomly, and so are taxonomically uninformative.

Grimmia reflexidens is a bipolar species widespread in the Northern Hemisphere, although uncommon in temperate Asia. In eastern North America it is rare, known only from a few localities in New Hampshire, New York, and Québec. It is the most common and widespread species of *Grimmia* in Antarctica, and it is relatively common in southern South America. Outside these two continents, it is rare in the Southern Hemisphere, known only from scattered localities in Australia, New Zealand, and Uganda.

Grimmia reflexidens (as *G. sessitana*) has been recorded from China by Cao and Vitt (1986: 166, fig. 21). I was able to study the materials on which their reports are based. Whereas some of the specimens from Chang Bai mountain are *G. reflexidens*, other collections from the same locality (e.g., *Cao Tong* 199, ALTA) are *G. longirostris*. The Yunnan specimen (*Zhu & Wu* 64082, ALTA) is *G. elongata*.

All authors except Deguchi (1978: 207) have mistakenly ascribed the authorship of *Grimmia lamellosa* to "Müll. Hal." (e.g., Greven, 1995; Wijk et al., 1962: 390; 1969: 655). In fact, Müller described *Guembelia lamellosa*. The reason for this mistake may be that in the original publication the genus *Guembelia* follows *Grimmia*, and Müller wrote out the full generic name only for the first species of each genus. For the remaining species he used the contractions "G." and "Gr." and this could have escaped the notice of later authors.

Selected specimens examined (533). UGANDA. Ru-

wenzori, Mijusi Valley, E slope of Mt. Speke, *O. Hedberg* 571 (PC, UPS).

ANTARCTICA. **Antarctic Peninsula Region:** André Island, Charlotte Bay, *Lewis-Smith* 4018 (IBA-7365). **Melchior Archipelago:** Fysted Island, Water Fanding, *Siple* 376.2 (FH). **Queen Mary Land:** Bunger Hills, in the neighbourhood of the Polish Base by the so-called "Totalizator," *Różycki s.n.* (IBA-7384). **Queen Maud Land:** Princess Astrid Coast, Drygalski Mts., NE slopes of the nunatak Malenkij, *Kononov s.n.* (IBA-7381). **Ross Sector:** Cape Sastrugi, *Walton* 227 (IBA-7382). **South Shetland Islands:** King George Island, Admiralty Bay, Skua Cliff above Petrified Forest Creek, W of Arctowski Station, *Ochrya* 627/80 (NY). **Victoria Land:** Cape Adare, *Terra Nova Expedition s.n.* (IBA-7379). SOUTH GEORGIA. Grytøcken, "Dammen," 4 Apr. 1933, *Jrøim s.n.* (BM).

AUSTRALIA. **New South Wales:** Mt. Kosciusko, Merri's Camp, *Maiden & Forsyth* 203 (H-BR). NEW ZEALAND. **North Island:** Pinales Ridge, Mt. Ruapehu, Feb. 1942, *Sainsbury s.n.* (BM). **South Island:** Tasman Glacier, near De La Beche Hut, *Sainsbury* 756 (BM).

AFGHANISTAN. **Parwan:** Panjskir valley, *Ruka*, 10 Oct. 1948, *Köie s.n.* (ALTA). ANDORRA. Riu de la Coma del Forcat, *Casas s.n.* (BCB-21723). AUSTRIA. **Carinthia:** in alpe "Fasibaunernik," pr. Malta, 1880, *Breidler s.n.* (TRH). **Salzburg:** Oblitzen bei Muhr im Lungau, *Breidler s.n.* (BP-36694). **Steiermark:** auf Glimmerschiefer "Speiereben bei Schöder," *Breidler s.n.* (BP-26598). **Tirol:** Sölden (am Ortler), Zaital, very near the Dusseldorferhutte, *Townsend* 92/547 (IBA-6280). BELGIUM. Spa, promenade Annette et Lubin, *Cornet s.n.* (BP-36284). BULGARIA. **Sofia:** Rila-Geb., Musalla, *Richard s.n.* (GLM-2851). CHINA. **Jilin:** Mt. Chang Bai, *Koponen* 36641 (ALTA). **Xinjiang** Uygur: Nileke Co., Haxilegen vicinity along Du-ku Highway, Tian Shan Range, *Zhao* 953267 (MO). CZECH REPUBLIC. Tatra Magna, in valle Kistarpatak-völgy, Malá Studená dolina, *Boros s.n.* (BP-112930). FRANCE. **Ariège:** Montreign, 7 Sep. 1923, *Culmann s.n.* (Z). **Hautes Alpes:** Lantaret, Combegnot, 21 July 1926, *Culmann s.n.* (Z). **Isère:** La Lauirtel, 17 Aug. 1894, *Theriot s.n.* (TRH). **Pyrenées Centrales:** au sommet du port d'Oo, 5 Sep. 1856, *Zetterstedt s.n.* (TRH). **Haute-Savoie:** Chamonix, *Payot s.n.* (TRH). GEORGIA. Imeretia, in alpe Chrshein, *Brotherus* 232 (H-SOL); distr.

Sukhumi, in vicinitate pagi Omarishara, in valle rivi Klich, 20 June 1986. *Vasák s.n.* (NY). GERMANY. Sutherland, *Sendtner s.n.* (GLM-12812). INDIA. **Himanchal Pradesh:** Bara-Lacha-La, Lahul, Kangra, Punjab, *Koelz 6774* (MO). ITALY. **Trento:** Pedergone di Trento, Oct. 1919, *Sbarbaro s.n.* (BM). JAPAN. **Honshu:** Mt. Tateyama, Toyama Prefecture, 11 Aug. 1955, *Iwatsuki s.n.* (H, JE). **Kyushu:** Kagoshima Pref., Kumage-gun, Isl. Yakushima, Mt. Miyanoura, *Mizokuti 59* (NICH-116232 p.p.). KAZAKSTAN. **Alma Ata:** Big Alma-Atynskoye Gorge and Lake, shore of Lake Alma Atynskoye Zalilislly Alatau, *Allen 10636* (MO). MONGOLIA. **Chobd-aimak:** Erdeneburen-somon, Pabhöhe, *Schubert M196* (MO). NORWAY. **Oppland:** Dovre pr. Kongsvold, *Kaurin s.n.* (BP-36229). **Sondre Trondhjems:** Opdal, pr. Sliper, 24 May 1883, *Kaurin s.n.* (TRH). PAKISTAN. Balistan, Rimochagma, *Duthie s.n.* (H). POLAND. Dolinka Buczynowa, *Chabubiński s.n.* (BP-36671). ROMANIA. **Hunedoara:** supra lacu Zenoga, montes Retezat, 3 Aug. 1969, *Vajda s.n.* (BP-74854). **Maramures:** in alp Pop-Jocac, ad Fochesány, *Margútai s.n.* (BP-112952). RUSSIA. **Dagestan:** Kasi-kumuk, Tschuly, July 1898, *Alexander s.n.* (H-BR). **Gorno Altayskaya Autonomous Oblast:** Altai Mountains, Kayakkatunarykskij Creek, *Ignatov 8/67* (IBA-7022). **Magadan:** Chukotka, Anadyr river basin, upper course of Ilmyneiveum river, 29 July 1978, *Afonina s.n.* (LE). SLOVAKIA, in jugo "Lorenz-Joch" supra lacum "Wahlenberg See," *Degen s.n.* (BP-86539); Höhe Tatra, Kleines Kohlbachthal auf der Lecwald, 10 Aug. 1905, *Gyoffry s.n.* (JE). SPAIN. **Ávila:** circo de Gredos, inmediaciones de la Laguna Grande, *Rupidera s.n.* (IBA-3985). **Gerona:** Coll dels Tres Pics, *Lloret s.n.* (BCB-25784). **Huesca:** Alta Ribagorça, pic de Salenques, *Ballesteros s.n.* (BCC-1276). **Lérida:** Vall de Bof, Comaloforno, *Ballesteros s.n.* (BCC-1277). SWEDEN. Torneträsk-området Abisko Nationalpark, Bergvegg, ovenfor Ridopakte, 11 Aug. 1945, *Gjäretröll s.n.* (TRH). SWITZERLAND. **Bern:** Unteraargletcher, *Trautmann s.n.* (BP-36682). **Graubünden:** 10 Sep. 1930, *Amann s.n.* (FH). **Rhaetia:** Davos, July 1887, *Amann s.n.* (TRH). **Tessin:** au lac de Muzzano, près de Lugano, 6 Sep. 1930, *Amann s.n.* (PC). TURKEY. **Malatya:** Taurus Cataonicus, In convallibus subalpinis prope vicum Bekikara inter urbem Malatja et vicum Kjachta, *Handel-Mazzetti 2422* (FH).

CANADA. **British Columbia:** shoulder of Storm Mountain, Vermilion Pass, 13 Aug. 1913, *Brinkman s.n.* (FH). **Québec:** Gaspé Co., Table-top Mt., *Collins 4378* (FH). U.S.A. **Alaska:** Kenai (A7) Quadrangle, Chisik Island, along shoreline about 0.5 mi. N of Cannery, *Talbot 407* (NY). **Arizona:** Cocconino Co., Point Sublime, on Fossil Shell Ridge, *Young 20* (MO). **California:** San Bernardino Mts., South Fork of Santa Ana, *Munz 6250* (FH). **Colorado:** Mesa Verde, *Lutz 4371* (FH). **Montana:** Flathead Co., Glacier National Park, along Sperry Glacier Trail, ¼ mi. E of Sperry Chalet, *Hermann 20709* (FH). **New Hampshire:** Mt. Washington, 10 July 1895, *Kennedy s.n.* (FH). **New York:** Essex Co., Keene, rocky summit of Gothics, *Miller 12045* (IBA). **Oregon:** Mt. Hood, 1 Aug. 1871, *Hall s.n.* (FH). **Washington:** Mason Co., near the summit of Mt. Ellinor, 13 June 1940, *Meyer s.n.* (G). **Wyoming:** Park County, Beartooth Lake Meadow, 20 Aug. 1953, *Conard s.n.* (MO).

ARGENTINA. **Santa Cruz:** in alpinis pr. Rio Tarde, *Halle 369* (BM). CHILE [no locality given], *Pöppig s.n.* (BM, JE). **La Araucanía:** Lonquimay, *Guenckel 1768* (PC). **Osorno:** Ottohsöhe, S Ufer des Lago Nahuel Huapi,

Schiller 25 (PC). **Santiago:** San Gabriel, Rto Maipo, *Looser 1037* (IBA).

9. **Grimmia ungeri** Jur., in Unger & Kotschy, Ins. Cypern. 169. 1865. *Grimmia alpestris* subsp. *ungeri* (Jur.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7: 112. 1883. *Grimmia alpestris* var. *ungeri* (Jur.) Husn., Muscol. Gall. 129. 1887. TYPE: [Cyprus.] In Olimpo Cypru, Vere [spring] 1862, *Unger s.n.* (lectotype, here designated, BM; isoelectotypes, BM [2 replicates], GOET [2 replicates], H-SOL, S).

Grimmia brachyodon Austin, Bull. Torrey Bot. Club 6: 45. 1875. *Grimmia montana* var. *brachyodon* (Austin) Lesq. & James, Man. 145. 1884. TYPE: "*Grimmia montana*, var. Sulliv. & Lesqx. Exsic. Ed. 2, n. 215 pro parte" [Sullivant & Lesquereux, Musci boreali-americi ed. 2, n. 215 (1865 [1866])] (lectotype, here designated, FH; isoelectotypes, FH [4 replicates], G, H, NY).

Grimmia jamesii Austin, Bull. Torrey Bot. Club 6: 43. 1875. *Grimmia montana* var. *truncata* Lesq. & James, Man. 145. 1884. TYPE: [U.S.A.] Nevada: Carson, *Watson 1412* (lectotype, here designated, FH; isoelectotypes, FH [2 replicates]).

Grimmia microtricha Müll. Hal. & Kindb., in Macoun & Kindb., Cat. Canad. Pl. 6: 70. 1892. TYPE: [Canada.] British Columbia: Revelstoke, 7 May 1890, *Macoun s.n.* (lectotype, here designated, S; isoelectotype, CANM-198087).

Grimmia montana var. *idahensis* Renauld & Cardot, Bot. Gaz. 30: 18. 1900. TYPE: [U.S.A.] Idaho: lac Pend d'Oreille, 1892, *Leiberg s.n.* (lectotype, here designated, PC; isoelectotypes, CANM-197540, FH [2 replicates], NY).

Grimmia pseudomontana Cardot & Thér., Bot. Gaz. 30: 18, Pl. IV fig. 2. 1900. TYPE: [U.S.A.] Idaho: near Moscow, 24 Mar. 1894, *Henderson s.n.* (lectotype, here designated, PC).

Grimmia canadensis H. Winter [Karl Herman Winter, 1845-1933; as cañadensis], Hedwigia 55: 102, fig. 4. 1914, nom. illeg., non Kindb., 1897. *Grimmia ovalis* subsp. *canadensis* (H. Winter) Podp., Consp. Musc. Eur. 279. 1954. TYPE: [Spain. Santa Cruz de Tenerife:] Tenerife Island, Cañadas del Teide, 2000 m. Apr. 1912, *Winter s.n.* (lectotype, here designated, JE; isoelectotypes, JE [5 replicates]).

Illustration. Figure 18.

Autoicous. Plants in tufts, olive-green to blackish. Stems to 1.5 cm tall, with central strand weakly developed; *axillary hairs* 5-8-celled, 105-175 μ m long. *Leaves* erect and appressed when dry, patent and rigid when moist, 1-1.7 \times 0.3-0.5 mm, ovate, acute, weakly keeled in the distal half, plane; *margins* plane proximally and incurved distally; *costa* semi-terete, prominent on the dorsal surface, although only weakly so above, slightly to clearly delimited; *lamina* 2-3(4)-stratose in the distal half, smooth; *distal cells* 5-7 μ m, isodiametric, plane or slightly bulging on dorsal surface, smooth; *proximal*

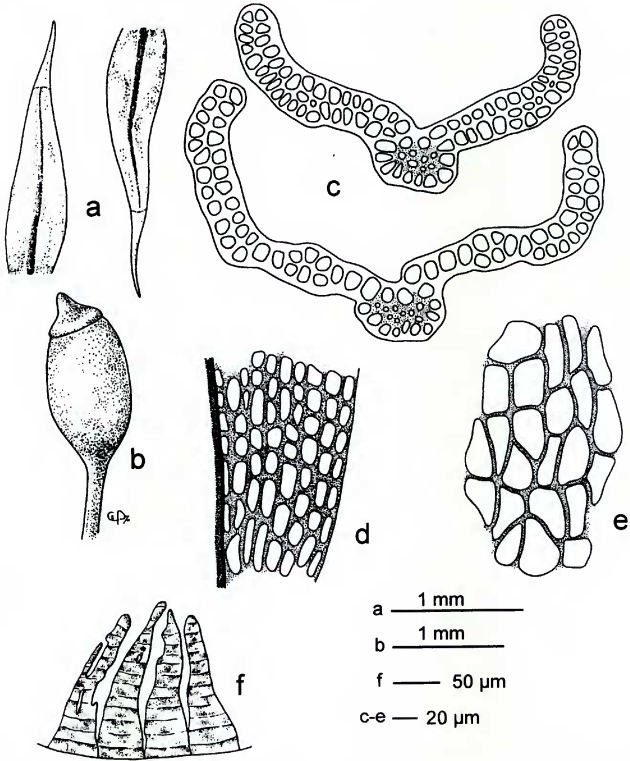


Figure 18. *Grimmia ungeri*. —a. Leaves. —b. Capsule. —c. Transverse sections of leaf. —d. Proximal leaf cells. —e. Medial exothelial cells. —f. Peristome teeth. [a–f. *Unger s.n.* (BM).]

paracostal cells 20–35 × ca. 16 μm, isodiametric to rectangular (1–2:1), with straight walls uniformly thickened or the transverse walls thicker than longitudinal walls; *proximal marginal cells* 10–25 × 6–10 μm, isodiametric to rectangular (1–2:1), with the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.7 mm long, smooth. *Perichaetial leaves* 1.5–2.5 × 0.5–0.9 mm, convolute and larger than vegetative leaves (2–3×); *hyaline hair-points* terete, straight, to 1.5 mm long, nearly smooth. *Androecia* terminal. *Setae* erect and straight, ca. 2 mm long.

Capsules exserted, ovoid or ellipsoid, symmetric, smooth, stramineous to brownish, lacking stomata; *exothelial cells* 17–65 × 13–45 μm, isodiametric and rectangular intermingled, thin-walled; *annulus* simple and persistent; *peristome teeth* 40–50 μm wide at the base, entire or moderately cribrate at the apex, orange-brownish, concolorous with the urn; *opercula* mammillate; *calyptrae* cucullate. *Spores* 9–13 μm.

Diagnostic characters. (1) Costa slightly prominent on the dorsal surface. (2) Laminal cells not bulging or only slightly. (3) Plants autoicous. (4)



Figure 19. Distribution of *Grimmia ungeri*.

Capsules lacking stomata. (5) Opercula mammillate.

Distribution (Fig. 19). North America, Europe, Cyprus, and Canary Islands; coniferous forests and open areas between 600 and 3900 m elevation, on metamorphic and igneous rocks, (either basalts or granites). Mature sporophytes were present in 89% of the specimens studied.

Grimmia ungeri is the only species in the genus so far known to combine an autoicous sexual condition with capsules lacking stomata. Unfortunately, the perigonia usually arise on different branches than the perichaetia and are usually difficult to find.

Grimmia ungeri has been included in the synonymy of *G. alpestris* almost since its original publication. However, it is closer to *G. reflexidens* or *G. montana* and is only remotely related to *G. alpestris*. From *G. montana* it is distinguished by its autoicous (rather than dioicous) sexual condition and its obtusely mammillate opercula. *Grimmia reflexidens*, also autoicous, has stramineous urns contrasting strongly in color with the orange peristome teeth, and the capsules have stomata at the base. The remaining species in section *Montanae*, *G. alpestris*, *G. caespiticia*, and *G. nivalis*, differ in having bulging laminar cells, whereas members of section *Donnianae* are distinguished by their proximal laminar areolation.

Grimmia ungeri exhibits a rather anomalous distribution pattern. In North America, it is common along the Pacific Coast, but very rare on the Atlantic Coast, with only one locality known (in Québec). In Europe, it is known only from single localities

in Scotland and Sardinia. From Africa *Grimmia ungeri* is also known from just one locality in the Canary Islands, from where it was described as *G. canadensis*. It also occurs in Cyprus, where it is common.

Greven (1995) considered this species as endemic to Cyprus and suggested that the remaining European records pertained to *G. alpestris* or *G. reflexidens* (as *G. sessitana*). However, the European collections are morphologically identical with Cypriot and North American plants.

The protologue of *G. brachyodon* states "*Grimmia montana*, var. Sulliv. & Lesqx. Exsic. Ed. 2, n. 215 pro parte" as the type of the taxon. The label of the specimen n° 215 of Sullivant and Lesquereux's exsiccata reads: "California: montis Diablo (Bolander); etiam in albus Sierra Nevada montium (Brewer)," but in none of the studied sets is the material separated according to either the provenance or the collector.

Selected specimens examined (135). CYPRUS. In Olympo (Troodos) Cypri, *Unger s.n.* (S). ITALY. **Sardinia**: Ostseite der Pla. La Marmara (Mt. Gennargentu), 2 June 1906, *Herzog s.n.* (JE). SPAIN. **Santa Cruz de Tenerife**: Tenerife, Cañadas del Teide, Apr. 1912, *Winter s.n.* (JE). UNITED KINGDOM. **Scotland**: Aberdeenshire, Ballater, Mt. Curtin, July 1870, *Fergusson s.n.* (FH).

CANADA. **British Columbia**: head of Baker Creek, Jakmia River, Cascade Mts., 17 Oct. 1880, *Watson s.n.* (FH). **Québec**: Gaspé Co., Mt. Albert, *Collins 3961* (FH). MEXICO. **Baja California**: Las Cuevitas, Sierra Juárez, ca. 10 mi. S of Laguna Hanson, *Wiggins 9177* (FH). **México**: Mt. Popocatepetl, *Kiener 18591* (FH). U.S.A. **California**: Luyo Co., Rock Creek, *MacFadden 17386* (FH). **Colorado**: Tolland South Boulder Canyon, 18 July 1923, *Roberts s.n.* (FH). **Idaho**: Coeur d'Alene Mountains, Clearwater-St. Joseph divide, *Leiberg 1692* (S). **Montana**: Columbia Falls, 24 June 1895, *Williams s.n.* (S). **Nevada**: Carson City, 1868, *Watson s.n.* (FH). **Oregon**: Klamath Co., Odell Lake, 23 June 1931, *Howell s.n.* (FH). **Washington**: Ellesburg, 23 July 1916, *Bailey s.n.* (FH). **Wyoming**: Park Co., Shoshone Natl. Park, at "Three Mile Campground" area, off Hwy. 16, *Churchill 5845* (G).

PUBLISHED NOMINA NUDA

Grimmia alpestris Schleich., Neues J. Bot. 1: 196. 1806[1805] (= *G. alpestris*).

Grimmia caespiticia f. *epilosa* Pilous, Musci čechoslovenici exsiccati n° 483 (= *G. caespiticia*).

Grimmia holmiensis Lindb. ex Hartm., Handb. Skand. Fl. Ed. 7: 374. 1858 (= *G. montana*).

Grimmia intermedia Fergusson, in Braithw., J. Bot. 10: 198. 1872 (= *G. ungeri*).

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